RHYTHM IN HUMAN COGNITION AND ACTION: HEALTH AND PATHOLOGY

EDITED BY: Charles-Etienne Benoit, Floris Tijmen Van Vugt, Laura Ferreri
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RHYTHM IN HUMAN COGNITION AND ACTION: HEALTH AND PATHOLOGY

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Editorial: Rhythm in human cognition and action: Health and pathology

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Editorial on the Research Topic
Rhythm in human cognition and action: Health and pathology

As a group of young scientists building their careers doing research in the cognitive science of music, we saw over the past decade how the field grew more legitimate. In this line of research, the study of rhythm in humans presents a long and rich scientific history which increasingly demonstrates the positive impacts of rhythm-driven enhancement at both neural and behavioral levels.

When we first launched the special issue "*Rhythm in Human Cognition and Action: Health and Pathology*", we wished to highlight the wide range of benefits that engaging with rhythmical events can generate: as a means to boost motors, cognitive, social and communication abilities. Looking back on the work in this special issue, we can clearly state that our goal was met: several research teams around the globe representing all these areas of research answered the call (51 authors published altogether 10 articles, representing 34 affiliations from 14 countries). Through this editorial article, we wish to survey the cohesion in which rhythm permeates so many aspects of our life. In particular, the current Research Topic collects several articles offering an updated view of the plurality of approaches in the study of rhythm in human cognition, ranging from experimental to clinical and social perspective. The issue will include a series of original reports and reviews that offer a comprehensive picture of the multifaceted interplay between rhythm and human functioning.

Indeed, perception, action, and cognition are strongly linked: the article by Fiveash et al. brings into light that rhythm perception involves strong auditory-motor connections that can be enhanced with movement. They investigated if a visual cue moving in time with regular rhythms could enhance the rhythmic priming effect. They demonstrate that on the contrary, visual over auditory cues could hinder the effect by potentially creating a dual-task situation.

The article published by Cochen De Cock et al. echoes these findings and shows that with the use of an auditory cue in the form of music can be used in a personalized rhythmical training to reinforce gait patterns in Parkinson's patients. This approach can also reduce fear of falling and improve the patients' overall quality of life. This was made possible by using a portable phone-based application aligning the musical tempo in real time to optimize gait.

The work by Ravi et al. further presents the link between rhythm and locomotion. They argue that movement circuitry contributes to the continuous regulation of our walking rhythm, even in the presence of perturbations that can destabilize locomotion. Temporal adaptation to perturbations provides an understanding of the link between rhythm and balance while their results extend on the sensorimotor synchronization paradigm toward improving our understanding of an individual's resilience to perturbations and potential fall risk.

The importance of sensorimotor synchronization in health is explored in more depth in the review article by von Schnehen et al. showing that such a therapeutic approach is able not only to benefit in a large array of neurocognitive disorders, but also to bring positive changes in healthy aging. This work also synthesizes the brain and cognitive mechanisms involved in these known benefits.

The article by Verga et al. expands on this neurocircuitry and demonstrates that traumatic brain injuries to these important brain areas create dysfunctional timing. They suggest that basic co-occurring perceptual and motor timing impairments may factor into a wide range of daily activities.

One such daily activity is our ability to move. The article by Ferreri et al. emphasizes that a regular rhythmic stimulation increases people's ability to anticipate future events in time and to move their body in space. Their findings support the idea that temporal predictions driven by a regular auditory stimulation are grounded in a perception-action system integrating temporal and spatial information.

The transferability of sensorimotor synchronization can be extended to the area of language. The article by Kertész and Honbolygo demonstrates that tapping to music predicts literacy skills of first-grade children. Their results show that phonological awareness, spelling and reading accuracy were associated with the musical tasks while reading fluency was predicted. Language by itself is a social endeavor: more facets of our social interactions are influenced by rhythm.

Indeed, moving together in time affects human social affiliation and cognition. The work by Basile et al. investigates if these effects extend to on-line video meetings through the lens of empathy or the theory of the mind. They concluded that participants in synchronous movement rated feeling greater closeness and similarity to their partners relative to an asynchronous condition, and that this influences social affiliation measures.

When looking at social interactions, people coordinate not only at the behavioral, but also at the physiological and neural levels, and that this coordination gives a temporal structure to the individual and social dynamics. Farrera and Ramos-Fernandez review the evidence for the existence of group-level rhythmic patterns that result from social interactions and argue that the complexity of group dynamics can lead to temporal regularities that cannot be predicted from the individual periodicity leading to an emergent collective rhythm.

Finally, from a mathematical modeling standpoint, it has been observed that the frequency of participants' oscillations reduces when compared to that acquired in solo. Calabrese et al. aim at capturing this phenomenon by proposing three alternative modifications of the standard Kuramoto model often employed to model human synchronization.

Taken together, these works show how rhythm broadly affects human functioning. This question is approached through a wide range of different perspectives, from experimental studies to modeling and reviews. We want to thank all the authors for their splendid contributions that push the boundaries in our understanding of the complex interactions between many facets of human experience.

Author contributions

All authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

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ORIGINAL RESEARCH
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BeatWalk: Personalized Music-Based Gait Rehabilitation in Parkinson's Disease

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Taking regular walks when living with Parkinson's disease (PD) has beneficial effects on movement and quality of life. Yet, patients usually show reduced physical activity compared to healthy older adults. Using auditory stimulation such as music can facilitate walking but patients vary significantly in their response. An individualized approach adapting musical tempo to patients' gait cadence, and capitalizing on these individual differences, is likely to provide a rewarding experience, increasing motivation for walk-in PD. We aim to evaluate the observance, safety, tolerance, usability, and enjoyment of a new smartphone application. It was coupled with wearable sensors (BeatWalk) and delivered individualized musical stimulation for gait auto-rehabilitation at home. Forty-five patients with PD underwent a 1-month, outdoor, uncontrolled gait rehabilitation program, using the BeatWalk application (30 min/day, 5 days/week). The music tempo was being aligned in real-time to patients' gait cadence in a way that could foster an increase up to +10% of their spontaneous cadence. Open-label evaluation was based on BeatWalk use measures, questionnaires, and a six-minute walk test. Patients used the application 78.8% (±28.2) of the prescribed duration and enjoyed it throughout the program. The application was considered "easy to use" by 75% of the patients. Pain, fatigue, and falls did not increase. Fear of falling decreased and quality of life improved. After the program, patients improved their gait parameters in the six-minute walk test without musical stimulation. BeatWalk is an easy to use, safe, and enjoyable musical application for individualized gait rehabilitation in PD. It increases "walk for exercise" duration thanks to high observance.

Clinical Trial Registration: ClinicalTrials.gov Identifier: NCT02647242.

Keywords: Parkinson's disease, cueing, rhythmic auditory stimulation, physical activity, gait rehabilitation, precision medicine BeatWalk

INTRODUCTION

In patients with Parkinson's disease (PD), physical activity has positive effects on strength, balance, gait and quality of life (Lauze et al., 2016; Porta et al., 2018). Instead of engaging in physical activity, however, patients report being one-third less active compared to healthy older adults (van Nimwegen et al., 2011). Reduced physical activity can even initiate a cycle of deconditioning and progressive disability, independent of latent disease progress, worsening motor and non-motor symptoms of PD (van Nimwegen et al., 2011).

Different factors such as perceived self-efficacy and enjoyment influence patients' involvement with physical activity (Urell et al., 2019). In particular, enjoyment plays a critical role in maintaining physical activity over time and in improving the quality of life (Urell et al., 2019). The clinical setting in which patients perform physical activity may not always be very motivating. Hence, there is an urgent need for alternative and more motivating strategies to promote physical activity in PD. Here we propose that walking with music, while exercising outdoor in a non-clinical setting, is a viable, enjoyable, and motivating alternative. Our approach is coupled with the use of mobile technologies capable of providing performance feedback, an important aspect of motivation in physical activity (Ginis et al., 2016) seldom proposed to patients.

Music and other rhythmic auditory cues have immediate as well as longer-term beneficial effects on gait parameters in PD (Thaut et al., 1996; Ghai et al., 2018). Yet, PD symptoms are highly heterogeneous, and the effects of music stimulation can vary significantly among studies (de Dreu et al., 2012) and patients (Dalla Bella et al., 2017; Cochen De Cock et al., 2018). We recently showed that the variable response to rhythmic cues is linked to inter-individual differences in rhythmic abilities (Cochen De Cock et al., 2018; Dalla Bella et al., 2018). Indeed, difficulties in rhythm perception and synchronization common in PD (Grahn and Brett, 2009; Benoit et al., 2014; Bienkiewicz and Craig, 2015) are likely to negatively modulate otherwise positive effects of musical rhythm on movement (Dalla Bella et al., 2017; Cochen De Cock et al., 2018; Dalla Bella, 2020).

There is growing evidence that individualized and interactive music or rhythm stimulation strategies that foster spontaneous entrainment hold some promise in improving gait performance (Hove et al., 2012; Dotov et al., 2019). In these strategies, the stimulus is modified in real-time so that its beat is dynamically aligned to the patient's steps. Spontaneous entrainment fosters a more natural, paced walking experience. More importantly, it avoids the need for instructed purposeful beat-step synchronization, a solution that is not always beneficial (Ready et al., 2019).

In this study, we tested a new personalized music-based gait rehabilitation protocol embedded in a smartphone application, called BeatWalk. The stimulation is interactive and aims to find the optimal compromise between individual patient's capacities and stimulus features, by building on coupled-oscillators modeling of gait temporal dynamics (Damm et al., 2019; Dotov et al., 2019).

BeatWalk allows the patients to walk outdoor, with performance feedback, while listening to step-synchronized music of various genres. We hypothesized that the ratio benefits/risks of BeatWalk use is positive. To test this we measured observance, safety, tolerance, usability, and enjoyment as in a phase 2 clinical trial. We also examined how BeatWalk can promote physical activity.

PARTICIPANTS AND METHODS

Participants

Forty-five patients with PD (aged 65 ± 9; 25 males) exhibiting gait disorders but able to walk unaided (Item 10 of the MDS-UPDRS-III ≥ 1 and <3; Martinez-Martin et al., 2013), without freezing, were recruited from the Department of Neurology of the Beau Soleil Clinic and the Regional University Hospital of Montpellier (France).

Diagnosis was established according to the Queen Square Brain Bank criteria (Hughes et al., 1992). Six participants interrupted the study without using BeatWalk, two because of inability to use the application from the beginning, and four because of inability to walk for 30 min. They did not differ from the 39 other patients on age, sex, disease severity, treatment, and gait measures. Participants were kept on their usual medications during the evaluation. Disease severity was moderate (MDS-UPDRS-III = 26.71 ± 12.06, Hoehn and Yahr stage = 2.4 ± 0.5). Disease duration was 7.6 ± 4.6 years and age at onset 57.4 ± 10.2 years. Levodopa equivalent daily dose was 701 ± 441 mg (Tomlinson et al., 2010) and 66.6% of the patients received dopamine agonists, 37.7% monoamine oxydase inhibitors, 9% entacapone and none had anticholinergics.

The study was approved by the National Ethics Committee (CPP Sud Méditérannée III, Nîmes, France, ID-RCB: 2015-A00531-48). All participants gave written informed consent before participating.

PROCEDURE

Rehabilitation Program

Patients were asked to walk alone outside in a safe environment (with no cars, without crossing roads, and on regular ground) while listening to musical stimuli for 30 min, five times a week, for 4 weeks. During each session, they could stop up to four times and for maximum of combined 10 min.

BeatWalk Application (Figure 1)

BeatWalk includes a smartphone application (Garzo et al., 2018) that modifies the tempo of the music in order to induce spontaneous mutual synchronization with patients' gait (Dotov et al., 2019) and ankle-worn sensors. The procedure implemented in BeatWalk is illustrated in **Figure 1**. The music tempo was updated in real-time to match the patient's gait cadence calculated from the five most recent footfalls. Footfalls were detected by streaming angular velocities and accelerations of the lower limbs measured by inertial sensors to the smartphone. We selected the adaptation parameters such that the stimulus was interactive, but also left enough space for the participants to adapt to it, thus encouraging mutual synchronization.

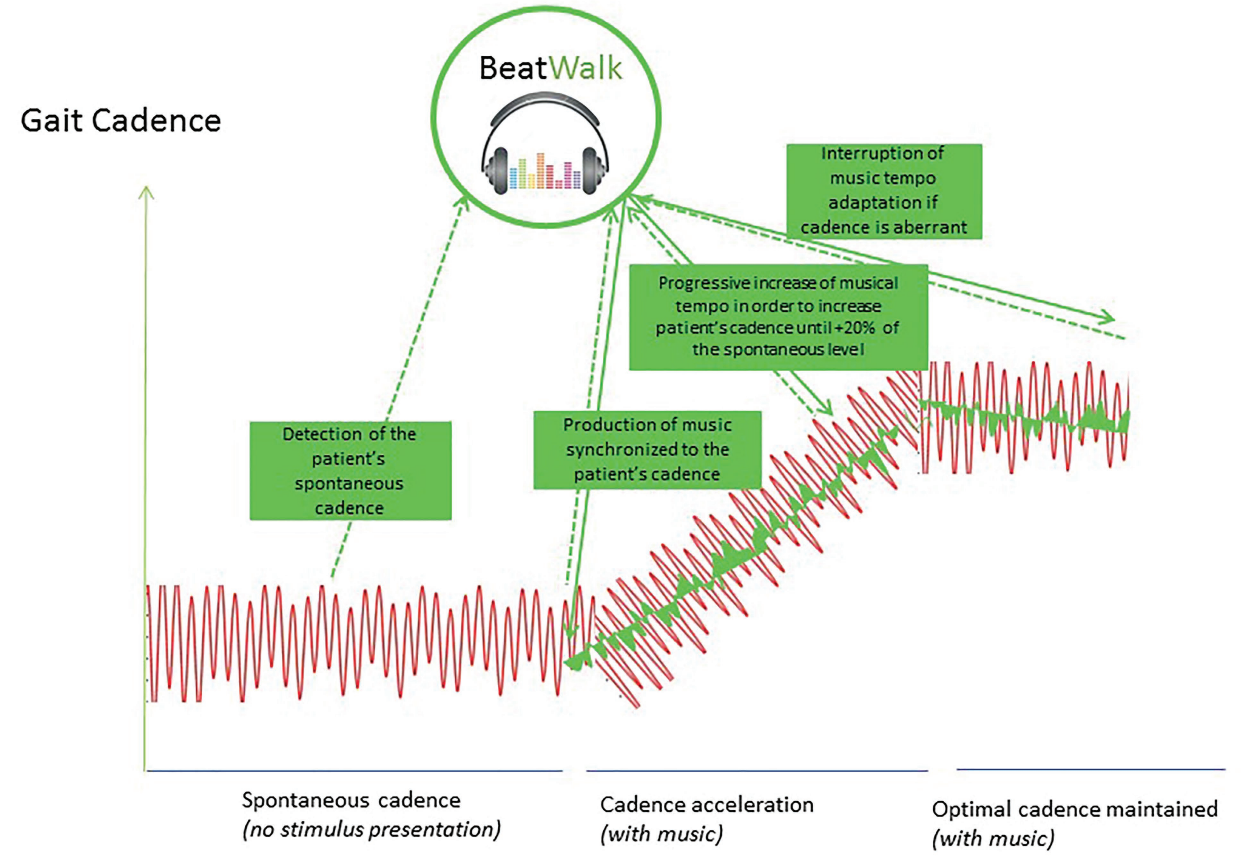


FIGURE 1 | BeatWalk operation: (1) first BeatWalk is silent and detects the patient's spontaneous gait cadence and phase, (2) BeatWalk generates music with a tempo synchronized to the patient's spontaneous cadence, (3) BeatWalk modifies subliminally the tempo of the music (changing the peace of music if necessary), to increase it progressively at maximum +20% of the patients spontaneous cadence, (4) BeatWalk maintains the tempo of the music in the targeted cadence range.

Using the participant's 1 min pre-test at each session as a baseline, we set the intrinsic tempo of the stimulus so that the effective compromise tempo where stimulus and gait met would be anywhere between 100 and 120% of baseline depending on the given participant's capacity to increase his or her cadence (Dotov et al., 2019).

The custom software played auditory tracks prepared in advance and paired with meta-information files annotated with beat times. We sorted 285 pieces of music in six genres (disco, pop, soft pop, pop rock, instrumental, and variety). Patients had to choose at least two genres for each session. The program applied online stimulus adaptation. To this end, a phase vocoder time-stretching algorithm modulated the song tempo without producing audible deformations of pitch (Moens et al., 2014). Time-stretching was controlled by the interactive stimulus oscillator using step phase and cadence computed online from the latest detected footfalls.

BeatWalk Interface (Figure 2)

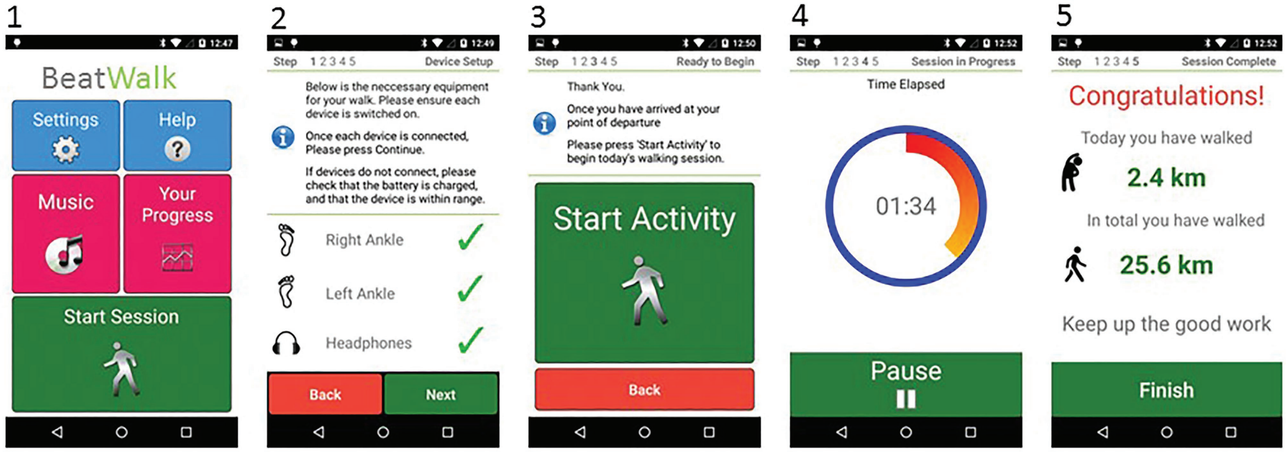
The application was designed (1) to increase the patient's motivation to walk, and, (2) to provide clear and simple instructions ensuring usability for patients with PD. The patient could choose the musical genre for each session. Encouraging feedback about session progress was provided during the session. At the end of each session, feedback was given about gait performance (e.g., gait speed, distance traveled) in the latest and all previous sessions (Garzo et al., 2018).

EVALUATIONS

Neurological and neuropsychological evaluations and gait measurements were performed before and after the 4-week rehabilitation program.

Neurological and Neuropsychological Evaluation

Demographic characteristics and medical history were collected in a preliminary interview. Severity of the disease was evaluated on the Hoehn and Yahr scale (Hoehn and Yahr, 1967) and the revised Movement Disorder Society-Unified Parkinson's Disease Rating Scale (MDS-UPDRS; Martinez-Martin et al., 2013). The levodopa equivalent daily dose was calculated (Tomlinson et al., 2010). Self-evaluation of the risk of falls



Below is the neccessary equipment for your walk. Please ensure each device is switched on.

Once each device is connected, Please press Continue.

If devices do not connect, please check that the battery is charged, and that the device is within range.

Thank You.

Once you have arrived at your point of departure

Please press 'Start Activity' to begin today's walking session.

Congratulations!

Today you have walked

2.4 km

In total you have walked

25.6 km

Keep up the good work

FIGURE 2 | BeatWalk interface: (1) starting screen, (2) sensors connection check, (3) session starting, (4) session progression, (5) encouraging feedback with performances.

was provided by the patients using the Falls Self-Efficacy Scale Score (Tinetti et al., 1990). Balance was evaluated using the Mini-BESTest (Franchignoni et al., 2010).

We evaluated global cognitive functioning with the Montreal Cognitive Assessment (Dalrymple-Alford et al., 2010), depressive symptoms, with the Beck Depression Inventory (Beck et al., 1961), anxiety with the Parkinson Anxiety Scale (Leentjens et al., 2014), apathy with the Lille Apathy Rating Scale (Dujardin et al., 2013), fatigue with Fatigue severity scale (Krupp et al., 1989), and quality of life using with EQ5-D (Schrag et al., 2000).

Safety and Tolerance

All patients completed a daily survey about their number of falls and about their fatigue and pain with visual sliding scales during the 2 weeks before rehabilitation (baseline evaluation) and during the 4 weeks of the program. They were also asked about other side effects.

Training Program Observance, Usability, and Enjoyment

Observance was calculated as the effective amount of time the program was used, expressed as the percentage of the prescribed use duration (10 h on total). Usability was evaluated using a scale proposed to evaluate smartphone interventions (Ben-Zeev et al., 2014). We also measured physical activity enjoyment associated with each session using the Physical Activity Enjoyment Scale (Mullen et al., 2011). Patients were asked to rate "How do you feel at the moment about the physical activity you have been doing" using a seven-point bipolar rating scale. Higher PACES scores reflect greater levels of enjoyment.

Physical Activity Evaluation

We explored physical activity before and during the program using a questionnaire developed for the Community Healthy Activities Model Program for Seniors (CHAMPS; Stewart et al., 2001). This questionnaire assesses the weekly frequency and duration of various physical activities typically undertaken by older adults and allows an estimation of physical activity caloric expenditure/week. This caloric expenditure was calculated for all specified physical activities, including those of light intensity and for activities of at least moderate intensity (MET value ≥ 3.0).

Gait Measurements

Gait spatiotemporal parameters were recorded during a six-minute walk test *via* sensors (inertial measurement units including 3D accelerometers and gyroscopes, MobilityLab, APDM Inc., Portland) strapped over the feet and anterior side of the left and right tibia, and sternum. Each patient was assessed at the same time of day in "on" condition, ~1 h after drug intake, to control for variations due to the drug cycle.

Statistical Analyses

Categorical variables were presented as percentages and quantitative variables as means and standard deviations (SDs). Results before and after the rehabilitation program were compared using a Wilcoxon signed-rank test. Chi-squared tests or Fisher's exact tests were used for categorical ones. Significance level was set at $p < 0.05$.

RESULTS

Observance

Patients used the application 78.8% (±28.2) of the prescribed duration. Only 7.7% of the patients ($n = 3$) used BeatWalk <25% of the prescribed duration and 48.7% ($n = 19$) used it more than 90%. Patients performed on average 15.9 ± 5.8 sessions (range: 1–20), out of the 20 sessions prescribed.

The average session duration was 29.71 ± 1.10 min (instructed duration: 30 min) and the mean distance traveled was 2.42 ± 0.53 km per session. The overall distance traveled by the patients was 39.2 ± 17.3 km. Patients with reduced observance of the program (lower than 50%, $n = 8$), as compared to other patients in the group ($n = 31$), showed greater fear of falling (FSESS: 34.00 ± 11.94 vs. 25.71 ± 7.67, $p = 0.05$), impairment in motor daily living (MDS-UPDRS-II: 14.86 ± 5.27 vs. 8.71 ± 6.46, $p = 0.02$), and lower quality of life (EQ5D: 9.14 ± 1.68 vs. 7.86 ± 1.27, $p = 0.05$) before the program. They did not differ at the 6-min walk test at baseline for speed, stride length, or cadence.

Safety and Tolerance

The number of falls per week did not increase due to BeatWalk use and longer times spent walking. On the contrary, the patients tended to show a lower number of falls during the rehabilitation program than they typically experienced in a week (0.22 ± 0.76 vs. 0.11 ± 0.46, $p = 0.07$). We also observed a reduction in the number of fallers during the last 2 weeks of the rehabilitation program compared to the 2 weeks of baseline (8.9 vs. 11.1%, $p = 0.01$).

During BeatWalk use the patients reported a reduction of pain relative to the baseline (2.80 ± 1.71 vs. 2.21 ± 1.57, $p = 0.02$).

Fatigue while using BeatWalk did not change compared to baseline, on visual sliding scale (3.22 ± 2.13 vs. 3.99 ± 1.95, $p = 0.3$) and on fatigue severity scale (32.65 ± 15.87 vs. 30.52 ± 13.53, $p = 0.5$).

Patients did not report other side effects.

Usability and Enjoyment

Patients' responses to the different items in the acceptability/usability tests are reported in **Figure 3**. The number of patients with positive responses on usability items was much higher than with negative responses (60.5 vs. 10.8%, $p < 0.001$).

The score obtained in the Physical Activity Enjoyment Scale was 29.21 ± 8.61 points (min 8 and max 56) after 1 week of use of BeatWalk and 90.3% of the patients experienced "sufficient levels of joy" (mean over 24; Mullen et al., 2011). Interestingly, this score and percentage did not change over time and remained as high after 1 month of use (respectively, 28.33 ± 8.46, $p = 0.2$, and 92.0%).

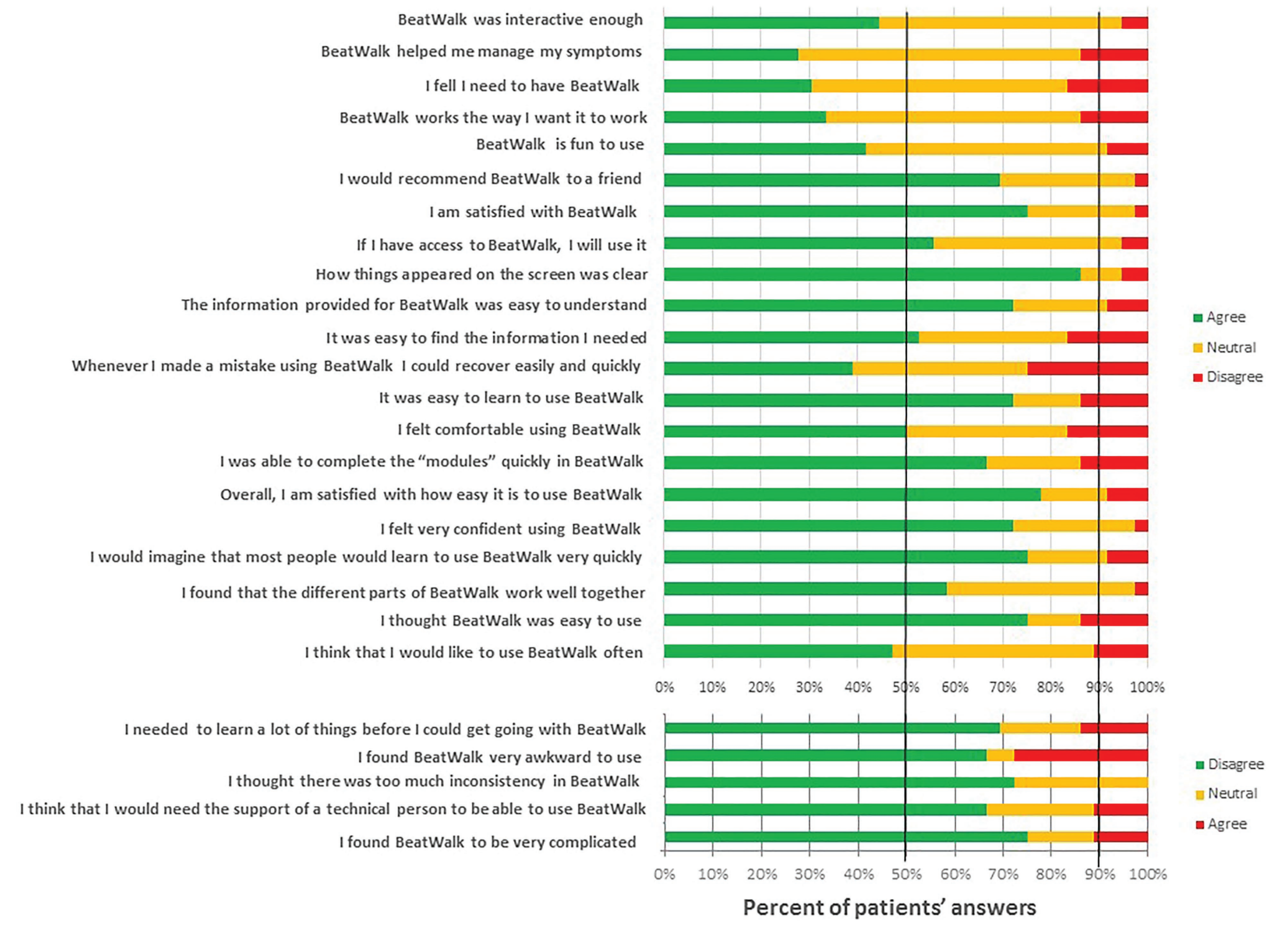


FIGURE 3 | Evaluation by the patients of different parameters of usability. In green responses favorable to BeatWalk, in orange, neutral, and in red unfavorable.

Quality of life and Self-evaluation of fall risk are reported in **Table 1**. Fear of falling decreased and the quality of life increased after the rehabilitation program using BeatWalk. However, it did not modify the severity of the disease or the neuropsychological and balance evaluations.

Physical Activity Evaluation

The frequency of physical activities and the associated caloric expenditures before and after the rehabilitation program are reported in **Table 2**. An increase was observed in the frequency of activities with at least moderate intensity and "walk for exercise." Caloric expenditure linked to "walk for exercise" and fast walk activities increased during the rehabilitation program.

Gait Parameters

Results on the 6-min walk tests taken pre- and post-intervention without auditory stimulation are reported in **Table 1**. An improvement was observed in distance, cadence, velocity, and stride length.

DISCUSSION

In this study, we demonstrated that our musical application (BeatWalk) for individualized gait rehabilitation in PD is a safe, user-friendly, and enjoyable solution displaying good observance. Practicing walking with it increases "walk fast" duration, confidence in gait, and quality of life. The application has been developed and tested first in a clinical setting, where it showed promising immediate effects on gait (Dotov et al., 2019). Using it at home in the context of a rehabilitation program was a new challenge, especially for patients with PD, who are mostly older adults and not always familiar with mobile technologies. Others have tested rhythmic cueing in rehabilitation in hospital (Dalla Bella et al., 2017) or at home but in the presence of a physiotherapist (Nieuwboer et al., 2007). Other studies were "mixed," with a part of the treatment performed at the hospital and another part at home without a physical therapist (e.g., Murgia et al., 2018). Our program differs from these protocols, as patients used the BeatWalk application alone at home and most of them managed to use it successfully, thanks to the adapted interface (Garzo et al., 2018). More than 75% of the patients found the application easy to use and would recommend it to a friend.

TABLE 1 | Clinical characteristics of patients with Parkinson's disease (PD) before and after treatment.

	Before rehabilitation program	After rehabilitation program	*P*
Number of participants	39	39	
Parkinson's disease evaluation			
Hoehn and Yahr	2.4 ± 0.5	2.5 ± 0.5	0.40
MDS-UPDRS-I	9.04 ± 6.27	7.67 ± 5.99	0.46
MDS-UPDRS-II	9.44 ± 6.50	9.71 ± 8.35	0.54
MDS-UPDRS-III	26.71 ± 12.06	22.87 ± 15.39	0.30
MDS-UPDRS-IV	4.11 ± 3.66	4.24 ± 3.66	0.67
Balance			
Falls self-efficacy score	26.87 ± 9.03	24.73 ± 7.86	0.05
Mini Best test	24.13 ± 3.12	24.73 ± 2.62	0.18
Quality of life			
EQ5D	7.89 ± 1.42	7.59 ± 1.57	0.03
EQ5D EVA	65.78 ± 16.99	66.76 ± 15.56	0.57
Psychological evaluation			
Depression (BDI)	11.53 ± 6.74	11.81 ± 8.43	0.91
Anxiety (PAS)	12.82 ± 7.16	12.84 ± 8.10	0.57
Apathy (LARS)	–7.3 ± 4.6	–9.0 ± 3.4	0.02
6-min test			
Distance	452.66 ± 75.39	470.29 ± 60.11	0.01
Cadence (steps/min)	118.01 ± 11.88	121.08 ± 10.13	0.01
Velocity (m/s)	1.28 ± 0.20	1.32 ± 0.17	<0.01
Stride length (m)	1.29 ± 0.13	1.31 ± 0.15	0.04
Asymmetry index (PCI, %)	5.42 ± 2.28	5.41 ± 2.46	0.49

MDS-UPDRS: Movement Disorder Society-Unified Parkinson's Disease Rating Scale, EQ5D: European Quality of life-5 Domains, BDI: Beck Depression Inventory, PSA: Parkinson Anxiety Scale, LARS: Lille Apathy Rating Scale, PCI: Phase Coordination Index.

The rehabilitation program using BeatWalk motivated patients to go outside, walk alone, and enjoy physical activity for almost eight and a half hours. Our patients' caloric expenditure, already quite high at baseline (Stewart et al., 2001), did not significantly increase during physical activity but rather reorganized so as to privilege "walk fast for exercise." This is probably more beneficial for the evolution of their disease.

The patients enjoyed performing physical activity with BeatWalk, a positive effect that was sustained for 20 sessions of gait rehabilitation. Combined with the personalized choice of the music genre, selecting music instead of a metronome for the stimulation might account for the patients' enjoyment ratings. Listening to music is an enjoyable and rewarding activity (Sihvonen et al., 2017), an effect mediated by the dopaminergic system (Ferreri et al., 2019). Enjoyment is both a predictor and outcome of physical activity participation (Dacey et al., 2008). Expected enjoyment from physical activities can increase exercise intentions, adoption, and maintenance (Dunton and Vaughan, 2008).

We recently reported that impaired rhythmic skills are associated with a poor immediate response to rhythmic cues (Cochen De Cock et al., 2018) and to a less pronounced longer-term effect of cueing in a rehabilitation protocol (Dalla Bella et al., 2017). The music delivered by BeatWalk is modified in real-time so as to temporally adjust the musical beats to the patients' steps. This interactive cueing was designed with the flexibility needed to induce synchronization in all patients, regardless of their rhythmic abilities. The spontaneous nature of entrainment implies that cognitive effort and deleterious effects of dual-tasking are minimized for patients. Interestingly, BeatWalk did not lead to a rise in the number of falls. The reduced double-tasking might also be part of this safety result. BeatWalk's response to gait information is twofold: (1) tempo is tailored to patients' cadence and (2) individual musical beats tend to slightly anticipate the footfalls. This subtle anticipation has a motivating effect and is part of how participants are induced to accelerate (Dotov et al., 2019).

TABLE 2 | Physical activity of patients with PD before and during BeatWalk rehabilitation program: caloric expenditure and frequency of exercises measured with the Community Healthy Activities Model Program for Seniors (CHAMPS) questionnaire.

	Before rehabilitation program	During rehabilitation program	*P*
Number of participants	39	39	
Caloric expenditure/week (kcal/week)			
in all exercise-related activities	3,793.9 ± 2,751.0	3,876.7 ± 2,714.7	0.9
in at least moderate intensity exercise-related activities	2,521.4 ± 1,766.2	2,693.0 ± 2,137.6	0.9
in “fast walk for exercise”	158.7 ± 348.6	528.4 ± 553.2	<0.005
Frequency/week			
of all exercise-related activities	22.0 ± 13.2	23.9 ± 9.1	0.3
of at least moderate intensity exercise-related activities	8.8 ± 7.1	11.3 ± 5.8	<0.001
of walk for exercise	0.8 ± 1.6	4.6 ± 1.8	<0.0001
Percent of participants			
who exercises with moderate intensity	89.7	100	<0.05
who walk for exercise	28.2	100	<0.001

BeatWalk delivers verbal feedback during the session. Participants also can follow their progress on the application screen. At the end of each session, the distance traveled and the mean speed of the latest and previous sessions were posted. This feedback has an important rewarding effect for patients and motivates physical activity (Ginis et al., 2016, 2017). Moreover, it could reduce fatigue, one of the main limiting effects of physical activity in patients with PD. Interestingly, in our study, the use of BeatWalk did not increase fatigue and patients completed almost all their sessions.

Fear of falling is common in PD (Lindholm et al., 2014). Self-efficacy, or the personal belief regarding the ability to perform a particular activity in a given situation, is an important factor of engagement in physical activity (Bandura, 1977). Fear of falling has already been identified as a barrier to physical exercise in PD (Ellis et al., 2013). Here, we demonstrated that patients who exhibited low observance to BeatWalk were those with increased fear of falling at baseline: fear of falling reduced the engagement in gait rehabilitation. Patients with a relatively high level of autonomy, probably felt more comfortable in using this tool. On the other hand, we also demonstrated that BeatWalk significantly reduced fear of falling and thus could facilitate exercise. Patients with increased fear of falling at baseline could benefit from gait rehabilitation with a physiotherapist prior to using BeatWalk. As such, the use of BeatWalk could initiate a virtuous circle for exercise and especially gait rehabilitation.

An increase in quality of life is another potential effect of the present intervention strategy. Physical activity is frequently associated with an improvement of quality of life in PD (Song et al., 2017), which has also been described in another gait rehabilitation program at home (Nieuwboer et al., 2007).

Another potential benefit of the present intervention strategy was not intended originally but became apparent with the recent sanitary crisis with COVID-19 pandemic infection. The requirements for confinement emphasized the need for auto-rehabilitation programs at home. Other intervention forms that may reduce impairments and improve quality of life are physiotherapy, occupational therapy, and speech therapy. Yet, these interventions require weekly sessions, impose stricter time and organizational constraints, and are not in compliance with current confinement restrictions, all of which represent a burden for the caregiver and the patients.

We observed non-controlled but encouraging results of efficacy on gait parameters in line with those observed in controlled studies by others (Nieuwboer et al., 2007; Dalla Bella et al., 2017) improving gait in the absence of stimulation.

This improvement can be the result of the increased physical activity associated with BeatWalk, supporting an improvement in muscular and cardiovascular capacities. It can also be the result of a restoration of the gait rhythmicity by the repeated use of music cueing, activating compensatory cerebello-thalamo-cortical loops, or increasing the activity of basal ganglia-thalamo-cortical circuits (Damm et al., 2019). Are these effects due to intrinsic motivational aspects of music, the rewarding effect of the interactive beat, or the constraints of a rehabilitation program, or a synergistic combination thereof? As encouraging as these results are, a large-sample randomized study currently in progress will compare walking in the absence of cueing (effect of physical activity), walking with music but no interactive cueing (motivating aspect of music), and walking with interactive music (reduced double-tasking and activation of the reward prediction mechanism).

CONCLUSION

BeatWalk is a new wearable application increasing “walk for exercise” in a generally sedentary population. The application delivered music interactively synchronized to the patients’ gait and proved to be safe, well tolerated, easy to use, and enjoyable. BeatWalk appears as a very promising tool for implementing music technology solutions for health care in patients with movement disorders.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by National Ethics Committee (CPP Sud Méditérannée III, Nîmes, France, ID-RCB: 2015-A00531-48). The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

The study was conceived and planned by VC, DD, FG, MP, VD, ED, BB, and SB. VC, DD, PI, FG, CL, AGi, VD, and CG collected the data. VC, SL, and SB analyzed and interpreted the data, and were involved in the initial drafting of the manuscript. VC, DD, LD, FG, MP, CG, AGa, EH, ML, ED, RV, BB, and SB revised the paper. All authors contributed to the article and approved the submitted version.

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Adapting Footfall Rhythmicity to Auditory Perturbations Affects Resilience of Locomotor Behavior: A Proof-of-Concept Study

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For humans, the ability to effectively adapt footfall rhythm to perturbations is critical for stable locomotion. However, only limited information exists regarding how dynamic stability changes when individuals modify their footfall rhythm. In this study, we recorded 3D kinematic activity from 20 participants (13 males, 18–30 years old) during walking on a treadmill while synchronizing with an auditory metronome sequence individualized to their baseline walking characteristics. The sequence then included unexpected temporal perturbations in the beat intervals with the subjects required to adapt their footfall rhythm accordingly. Building on a novel approach to quantify resilience of locomotor behavior, this study found that, in response to auditory perturbation, the mean center of mass (COM) recovery time across all participants who showed deviation from steady state (N = 15) was 7.4 (8.9) s. Importantly, recovery of footfall synchronization with the metronome beats after perturbation was achieved prior (+3.4 [95.0% CI +0.1, +9.5] s) to the recovery of COM kinematics. These results highlight the scale of temporal adaptation to perturbations and provide implications for understanding regulation of rhythm and balance. Thus, our study extends the sensorimotor synchronization paradigm to include analysis of COM recovery time toward improving our understanding of an individual's resilience to perturbations and potentially also their fall risk.

Keywords: time perception, motor control, fall risk, sensorimotor synchronization, sensory cues, recovery potential, movement timing, rhythm perturbations

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INTRODUCTION

The rhythmic alternation of the trunk and limbs is a distinctive, visibly apparent characteristic of human walking. To achieve this, numerous muscles in the body are cyclically activated in a coordinated sequence by neural commands. The precise location of the generation of these neural commands still remains a matter of debate (Dougherty and Ha, 2019), but accumulating evidence suggests the involvement of a distributed network of inter-neurons and motor-neurons in the spinal cord (Takakusaki, 2017; Grillner and El Manira, 2020). Together with descending supraspinal signals and other interacting sensory, vestibular pathways, this movement circuitry contributes to the continuous regulation of our walking rhythm, even in the presence of perturbations (Rossignol et al., 2006; Goulding, 2009; Aoi et al., 2010). Importantly, impaired regulation of rhythmic walking patterns results in either random or stereotypical behavior that limits one's ability to adapt to perturbations, as observed in subjects with an increased risk of falling (Callisaya et al., 2011; Hamacher et al., 2011), as well as in individuals suffering from movement disorders, e.g., Parkinson's disease (O'Boyle et al., 1996; Plotnik and Hausdorff, 2008; Ravi et al., 2020) or stroke (Balasubramanian et al., 2009; Krasovsky et al., 2013).

To investigate and identify subtle impairments in rhythmicity and its regulation related to clinical symptomatology, it is necessary to move beyond experiments involving observations during steady state walking, in order to challenge the underlying neuromuscular mechanisms (Full et al., 2002). As a result, one proposed approach has been to exploit the sensorimotor synchronization paradigm (Repp, 2005; Torre et al., 2010), which evaluates a subject's ability to match the rhythmic oscillations of a limb with an external (often auditory) stimulus, including infrequent temporal perturbations (where beats are presented earlier or later than expected). This paradigm therefore challenges the individual's inherent rhythmicity during walking and assesses the elicited adaptive motor responses (Chen et al., 2006; Roerdink et al., 2009; Pelton et al., 2010; Wagner et al., 2016; Forner-Cordero et al., 2019). The methodology has, in essence, several positive aspects: the effect of altering rhythms on walking behavior can provide controlled and reproducible access to non-steady-state behavior as encountered in the real-world (e.g., walking on uneven terrains, negotiating obstacles, etc.). Furthermore, listening to music or beats is able to activate motor networks and compensate for impaired internal timing, hence providing a viable vehicle for rehabilitation of movement disorders (Damm et al., 2020). In fact, synchronizing walking to steady metronome beats (without perturbation) has been shown to increase overall balance ability, and be effective for functional locomotor recovery of individuals with stroke (Lee et al., 2018), Parkinson's disease (Capato et al., 2020), and multiple sclerosis (Maggio et al., 2021).

Early studies investigating walking rhythm deficits using auditory perturbations focused on the modality of temporal correction, i.e., how quickly and/or accurately participants are able to adapt the timing of their footfalls to recover synchronization with the beat after perturbation (Roerdink et al., 2009; Pelton et al., 2010). Here, the main observed parameter is generally the rate or number of walking cycles to achieve convergence to pre-perturbation footfall synchrony. In synchronizing to rhythm-perturbed metronome beats, however, the maintenance of stable whole-body (center of mass, COM) movement patterns can directly influence the timing of footfall correction response to the perturbation. Importantly, the inverse effect of footfall corrections on the dynamic stability of walking remains unaddressed, hence overlooking the critical aspect inherent in this paradigm for understanding an individual's resilience to rhythm perturbations and falling (Ravi et al., 2021). In this respect, recent empirical work suggests that individuals may prioritize whole-body stability in the stepping process over producing large synchronization corrections at the expense of their balance control (Brauer et al., 2002; Chen et al., 2006; Wright et al., 2014; Roy et al., 2017). However, it is not immediately clear if corrections to footfall timing adjustments are similarly to be expected for the dynamics of the COM, since the position and velocity of the COM is constantly regulated relative to the foot placement to maintain walking balance (Hof et al., 2005, 2010; Wang and Srinivasan, 2014; Ignasiak et al., 2019).

Given the possibility that temporal corrections could destabilize an individual and even induce a fall, it is clearly necessary to better understand how rhythm perturbations affect walking stability. To date, no study has attempted to explicitly test this proposition. Importantly, the extent to which footfall rhythm influences stability may also depend on the rhythm perception ability of the participants [instructing poor rhythm perceivers to synchronize could incur instability (Ready et al., 2019)] and the magnitude of perturbations (Dotov et al., 2019). As more studies including rhythm perturbations are now emerging (Krasovsky et al., 2013; Wright et al., 2017; Geerse et al., 2020; Khan et al., 2020; Nijs et al., 2020), it is timely to identify the governing principles and detail the involvement of dynamic stability during movement adaptation to rhythm perturbations: hence addressing the fundamental question of how footfall rhythmicity interacts with whole-body balance during walking.

A hallmark of successful movement adaptation is faster return to steady state following a perturbation (Hadley et al., 2017). The ability to reliably measure recovery of movement behavior (i.e., resilience) would thus clearly provide an improved understanding of the relationships between task level synchronization outcomes (i.e., number of walking steps to return to footfall synchrony) and dynamic stability of walking (i.e., number of walking steps to return to steady state COM kinematics). In order to address this underlying question, we build upon the unique approach of Ravi et al. (2021) for quantifying an individual's COM recovery to steady-state patterns after a perturbation. Toward understanding resilience to rhythm perturbations during walking, this pilot study aimed to investigate the relationships between footfall rhythmicity, auditory perturbations, and dynamic stability. To achieve this, the quantification of resilience was applied after young adults were subjected to a beat delayed perturbation in a metronome sequence.

MATERIALS AND METHODS

Study Participants

Twenty healthy young adults [13 males and 7 females; with mean age: 24.9 (standard deviation SD: 2.3) years; height: 1.76 (0.07) m; mass: 72.7 (6.3) kg] with no history of neurological, orthopedic or other disorders that would affect typical walking patterns participated in this study. The protocol was approved by the local institutional review board (protocol #EK 2019-N-178) and all participants provided written informed consent prior to participating, in accordance with the Declaration of Helsinki.

Experimental Protocol

A single-belt treadmill (h/p/cosmos sports & medical gmbh, Nussdorf, Germany) and a 10-camera 3D optical motion capture system (100 Hz; Vicon Motion Systems, Oxford, United Kingdom) were used to record the participants' movement patterns. A lower body marker set consisting of 37 reflective markers (see **Supplementary Table 1** for anatomical landmarks) was used. Participants wore comfortable shoes and clothing, as well as headphones (Sennheiser HD280 pro, Sennheiser electronic GmbH & Co. KG, Wedemark, Germany) to provide auditory cues and reduce background noise. They were additionally secured with a ceiling-mounted harness (zero bodyweight support) with chest and pelvis straps as a safety precaution against trips and falls.

Baseline Condition

Participants first walked without any auditory stimulus (Baseline walking 1, BW1, 6 min) at their pre-assessed self-selected walking speed. Here, each individual's baseline step time (defined as the duration from the heel contact of one foot to the heel contact of the contralateral foot, **Figure 1A**) was evaluated using a custom algorithm based on foot velocity (O'Connor et al., 2007) to inform the auditory conditions for the cued trial. In general, 5-min rest breaks were provided between the trials.

Stimulus Preparation

From BW1, a subject-specific metronome audio-track (**Supplementary Audio 1**) was created in which the inter-beat intervals (IBIs) of the auditory metronome (0.1 s of the musical note A, sine wave with frequency 440 Hz) were matched to the mean step time. To induce rhythm perturbations, the created track was adjusted by embedding five perturbation intervals, with the IBI increased by 20× the standard deviation of the baseline step time ("perturbation magnitude") and introduced around 3 min into the track (**Figure 1B**).

Cued Condition

Participants were then explicitly instructed to maintain stepping synchronicity with the beats and continue walking normally despite possible alterations to the IBI timing throughout the trial. After providing sufficient time for subjects to practice walking to the provided beat, participants then completed 6 min of cued-walking (CW) listening to the metronome track, which included the planned auditory perturbation.

A further baseline walking trial (BW2, 6 min) without auditory stimulus was then completed by the participants.

Data Analysis

Recovery of COM to Steady-State Patterns

The vertical displacement time series of the sacrum marker [used as a simple approximation of the body COM (Yang and Pai, 2014) and herein referred to as COM] from the three walking trials [formulated as: $X_{BW1}(t)$, $X_{CW}(t)$, and $X_{BW2}(t)$] were used for further analysis in this study. In order to minimize the start-up effects on walking, the first 5 s of the data were removed from analysis. The data were low pass filtered using a 4th order Butterworth filter with a cut off frequency of 5 Hz and demeaned.

The resultant time series were reconstructed in state space (**Figure 1C**) using the time delay embedding procedure (Wurdeman, 2016; **Supplementary Methods 1**). State-space reconstruction of movement time series offers a representation of the underlying dynamics, as well as a geometric illustration of the intrinsic steady-state behavior. An embedding dimension (d) and time lag (τ) were determined from each time series and averaged across the three trials to create the state space vectors [e.g., $[X_{BW1}(t),\ X_{BW1}(t+\tau), \ldots, X_{BW1}(t+(\mathrm{d}-1)*\tau)]$]. Here, each vector is a state that represents the walking behavior at a specific time, t.

In order to determine each subject's resilience to rhythm perturbations and falling, the recovery of COM kinematics to steady state movement patterns was evaluated [using the methodology developed in Ravi et al. (2021)] as follows:

Determination of Steady State COM Using Baseline Walking 1

1. A centroid and reference trajectory (M) was first determined on a reduced state space [three dimensions: $[X_{BW1}(t),\ X_{BW1}(t+\tau),\ X_{BW1}(t+2\tau)]$. The centroid was found by taking the mean of the state space vectors, while M was evaluated by fitting an eight-term Fourier model to the reconstructed data. For every state space vector, the corresponding angle relative to the centroid was then calculated using the four-quadrant inverse tangent (Matlab function: "atan2d").
2. Around M, an ellipse at each integer angle (θ) between 0° and 359° was constructed (**Figure 1C**). Each ellipse was defined using the 50 nearest state space vectors as follows: The length of the semi-major axis of the ellipse was set to the largest standard deviation of the enclosed state space vectors from the three dimensions. The second largest standard deviation gave the length of the semi-minor axis.
3. When schematized, the ellipses adopt the shape of a three-dimensional torus that we term $T_{1\sigma}$. Step 2 was repeated to construct $T_{2\sigma}$ and $T_{3\sigma}$ using two and three times the previously determined standard deviations, respectively.
4. In the context of our analysis, the torus is a steady state region around the reference trajectory to which the COM may return and settle after a perturbation.

Evaluation of COM Recovery Using Cued Walking

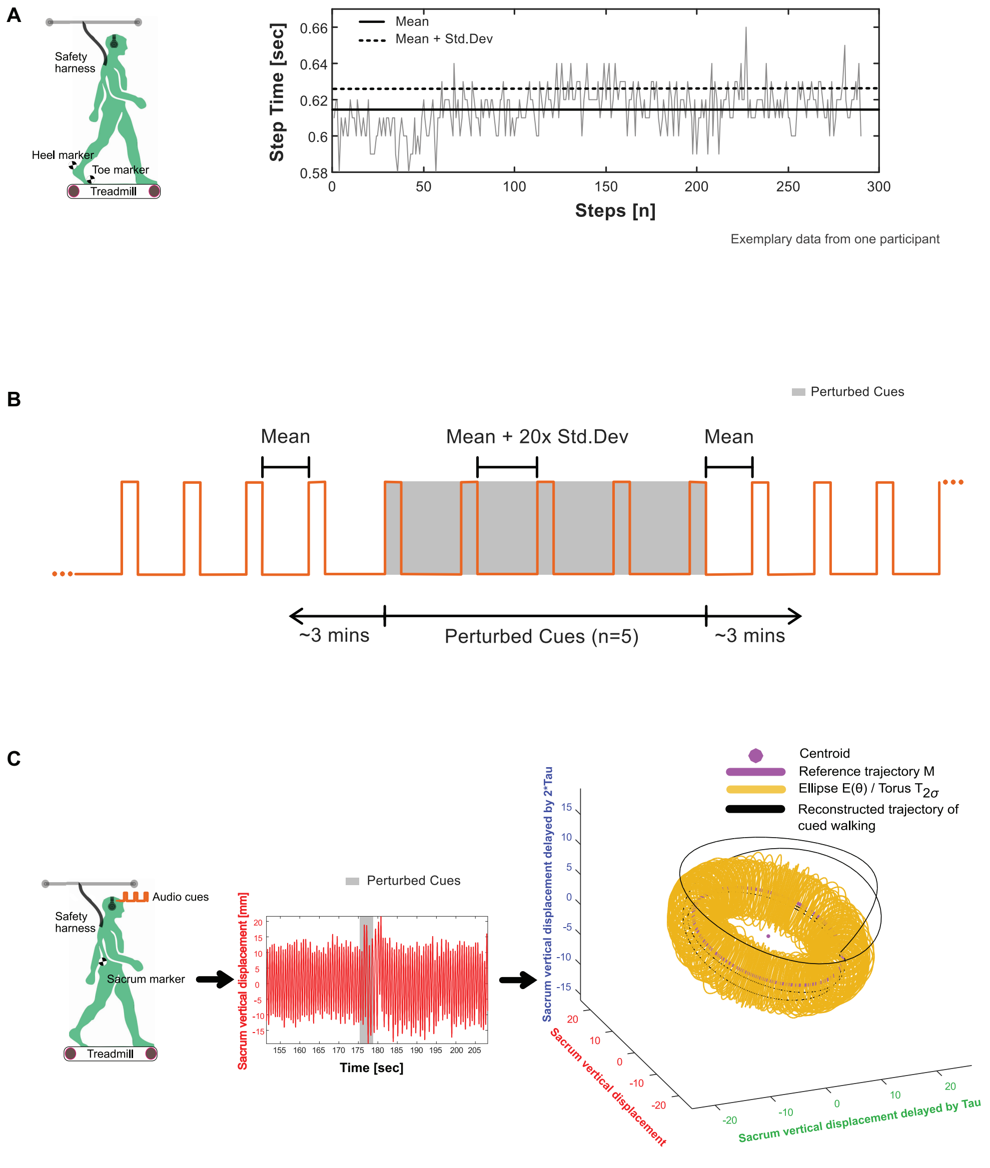
5. The reconstructed trajectory of $X_{CW}(t)$: $[X_{CW}(t), X_{CW}(t+\tau), X_{CW}(t+2\tau)]$ were now projected onto the tori (**Figure 1C**). The position of each state space vector was labeled according to the smallest constructed torus, $T_{1\sigma}$, $T_{2\sigma}$, or $T_{3\sigma}$ that enclosed that vector. Subsequently, the Euclidean distance, $D(t)$, of each state space vector to M was calculated (**Figure 2A**).
6. $D(t)$ was then parameterized using four variables adapted from Hadley et al. (2017), **Figures 2B–E**:

   Lag time (s) – interval between the start of the perturbation to the instant the reconstructed trajectory of $X_{CW}(t)$ leaves the torus $T_{2\sigma}$ for at least 0.1 s.

   Peak time (s) – interval after the lag time until the timepoint of maximum deviation of $D(t)$.

   Peak magnitude (mm) – magnitude of the maximum deviation.

   COM recovery time (s) – time interval from the time point of maximum deviation until the point of recovery. The point of recovery of COM was defined as the time point after which the trajectory no longer left the torus $T_{2\sigma}$ for five consecutive walking cycles (one walking cycle is equal to the duration between two consecutive heel contacts of the



For visualisation purposes, only Torus $T_{2\sigma}$ and only few gait cycles of cued walking are shown

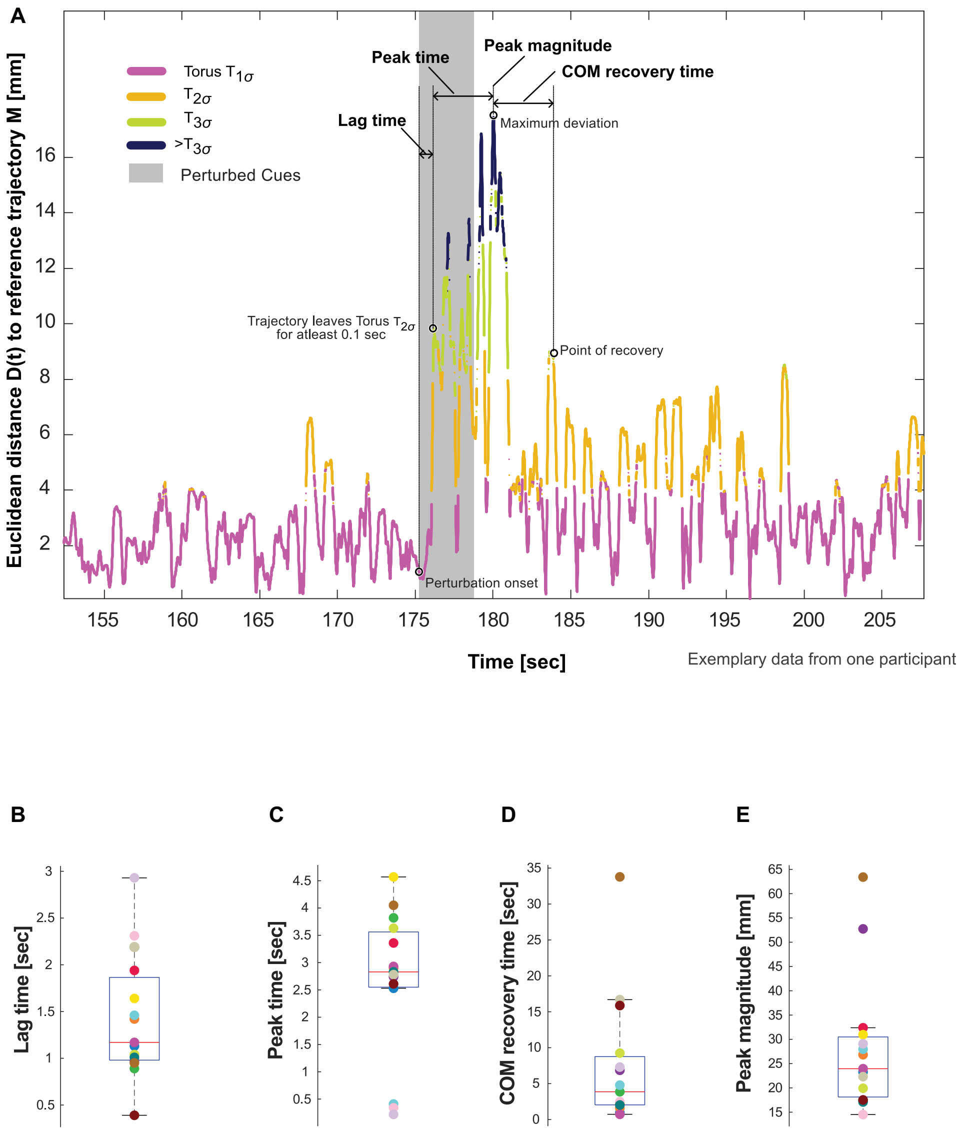
FIGURE 1 | Experimental procedure. **(A)** Extraction of average (mean and standard deviation) step time characteristics from baseline walking 1 (BW1) shown in an exemplary participant. The timing of heel strike and toe off, the events that mark the step time of walking were identified using a custom foot velocity algorithm. **(B)** Generation of subject-specific metronome audio-tracks using BW1 step time characteristics. The inter-beat intervals of the metronome were matched to the mean step time. To induce perturbations, the created track was adjusted by embedding five perturbation intervals, where the inter-beat intervals were increased by 20× the standard deviation of the step time and introduced around 3 min into the track. **(C)** Observation of perturbation response in an exemplary participant's center of mass movement (approximated in our study using the vertical displacement time series of the sacrum marker) with respect to their steady state boundaries given by the toruses (see section "Determination of Steady State COM Using Baseline Walking 1" in the manuscript for methodological details).

foot), permitting four outliers lasting no more than 0.01 s each (Ravi et al., 2021).

Participants' Aggregate Response to the Auditory Perturbation

In order to understand participants' aggregate response, the proportion of vector counts that were within ($T_{1\sigma}$, $T_{2\sigma}$, $T_{3\sigma}$) vs. those outside the boundaries ($>T_{3\sigma}$) were evaluated using the following additional steps:

7. Step 5 was repeated to evaluate $D(t)$ for the reconstructed data of BW2: $[X_{BW2}(t),\ X_{BW2}(t+\tau),\ X_{BW2}(t+2\tau)]$.
8. CW was divided into three phases: (1) start of the walking trial until the onset of the auditory perturbation (**CW**$_1$); (2) onset of auditory perturbation until COM recovery (**CW**$_2$);



Exemplary data from one participant

Data from N=15 participants labelled in different colours

FIGURE 2 | Resilience characteristics. **(A)** Evaluation of lag time, peak time, center of mass (COM) recovery time, and peak magnitude in an exemplary participant who showed deviation from steady state patterns in response to the auditory perturbation. Refer to Section "Evaluation of COM Recovery Using Cued Walking" in the manuscript for the definition and calculation of these characteristics. **(B–E)** Showcasing aggregate data for these characteristics using box plots with median, 25th and 75th percentiles, extreme values, and data from individual participants (*N* = 15).

(3) point of COM recovery until the end of the trial ($\mathbf{CW_3}$). The vector counts from CW, CW_1, CW_2, CW_3, and BW2 were aggregated for determining the duration within each torus ($T_{1\sigma}$, $T_{2\sigma}$, or $T_{3\sigma}$) and compared.

Recovery of Footfall Synchrony to Pre-perturbation Limits

Asynchronies were evaluated as the difference in time between the IBIs (i.e., mean step time from the BW1) and the step times obtained in CW. Pre-perturbation limits were quantified using the SD of the asynchrony from the 10 steps immediately preceding the perturbation [similar to the approach presented by Bank et al. (2011)]. To assess recovery of footfall synchrony following the auditory perturbation, a moving average window analysis was performed. For each window of three steps, mean asynchrony was calculated. The point of recovery of footfall synchronization corresponded to the middle step of the window for which the asynchrony fell within the reference range ± 2 SD of the pre-perturbation asynchrony and stayed within this range for at least eight consecutive windows (corresponding to 5 gait cycles or 10 steps). Synchrony recovery time was calculated as the period between the maximum step time adjustment (given by the peak of the asynchrony after the start of the perturbation) and the point of recovery of footfall synchronization.

Statistical Analysis

One-way repeated measures ANOVA was used to test for statistical differences in the d and τ values (dependent variables) of each participant between the trials (independent variable). Results were considered to be significant at an alpha of <0.05.

Aggregate data of Lag time, Peak time, Peak magnitude, and COM recovery time were reported as Mean (SD) and visualized using box plots. A stacked bar graph was used to represent relative vector counts between the tori and compared among CW, CW_1, CW_2, CW_3, and BW2.

Mean difference [confidence intervals] between COM recovery time and Synchrony recovery time were estimated. The bootstrap confidence intervals obtained using estimation stats gives a measure of precision and confidence about our estimate (Ho et al., 2019). All analyses were conducted in Matlab (v2020a, The MathWorks, Inc., Natick, MA, United States).

RESULTS

The average preferred treadmill walking speed was 3.7 (SD: 0.5) Km/h. The participants' mean step time during BW1 was 0.6 (0.01) s. Accordingly, the average perturbation magnitude and perturbation time were 0.26 (0.06) and 4.3 (0.5) s, respectively.

Effects of Filtering and Walking Conditions on Tau and Dim

There was no difference in τ and d between unfiltered and filtered data in any of the three walking trials, hence supporting the use of filtered data for state space reconstruction. The one-way ANOVA test confirmed that the differences in τ between walking trials did not reach statistical significance (τ: *F*-ratio value: 0.87, *p*-value: 0.43), while d remained unchanged. The average τ and d across walking trials was found to be 0.2 (0.02) s and 4, respectively.

Resilience Characteristics

Of the 20 participants analyzed, 5 did not show evidence of the effects of perturbation to COM kinematics (i.e., no deviation from $T_{2\sigma}$), and thus were excluded from further analysis. The remaining 15 participants showed an average lag time of 1.4 (0.7) s, peak time of 2.7 (1.3) s, and peak magnitude of 28.0 (13.5) mm. The perturbation resulted in an average COM recovery time of 7.4 (8.9) s (**Figure 2B** and **Table 1**).

Synchronization Characteristics

The attention and effort to synchronize to the perturbed auditory cues (and step adjustment responses) appeared to induce perturbations to the COM kinematics in the 15 participants who showed COM deviation from steady state patterns (**Figures 3A,B**). The maximum step time adjustment during CW (given by the peak of the asynchrony, section "Recovery of Footfall Synchrony to Pre-perturbation Limits") averaged at 0.16 (0.09) s.

TABLE 1 | Demographics, walking, resilience, and asynchrony characteristics.

Demographics (*N* = 20)	
Age (years)	Mean: 24.9 (SD: 2.3)
Height (m)	1.76 (0.07)
Mass (kg)	72.7 (6.3)
Male/female (*n*)	13/7
Treadmill speed (km/h)	3.7 (0.5)
First time on treadmill yes/no (*n*)	4/16
Baseline walking 1 characteristics (*N* = 20)	
Step time (s)	0.6 (0.01)
Perturbation magnitude (s)	0.26 (0.06)
Perturbation time (s)	4.3 (0.5)
Cued walking: resilience characteristics (*N* = 15)	
Lag time (s)	1.4 (0.7)
Peak time (s)	2.7 (1.3)
Peak magnitude (mm)	28 (13.5)
COM recovery time (s)	7.4 (8.9)
Proportion of total vector counts within $T_{1\sigma}$; $T_{2\sigma}$; $T_{3\sigma}$; $> T_{3\sigma}$ (*N* = 15)	
CW (%)	74.9 (14); 22.6 (11.6); 1.9 (2.3); 0.6 (0.5)
CW_1 (%)	77.8 (13.7); 20.8 (11.8); 1.3 (2); 0.1 (0.2)
CW_2 (%)	25.5 (9.8); 36.6 (13.4); 21.1 (8.6); 16.9 (12.8)
CW_3 (%)	74.6 (15); 23.8 (12.2); 1.6 (2.8); 0.1 (0.2)
BW2 (%)	75.9 (7); 22.9 (6.4); 1.2 (0.8); 0.1 (0.1)
Asynchrony characteristics (*N* = 15)	
Synchrony recovery time (s)	4 (2.1)
Differences in COM recovery time relative to synchrony recovery time (s)	Mean difference: +3.4 [CI: +0.1, +9.5]

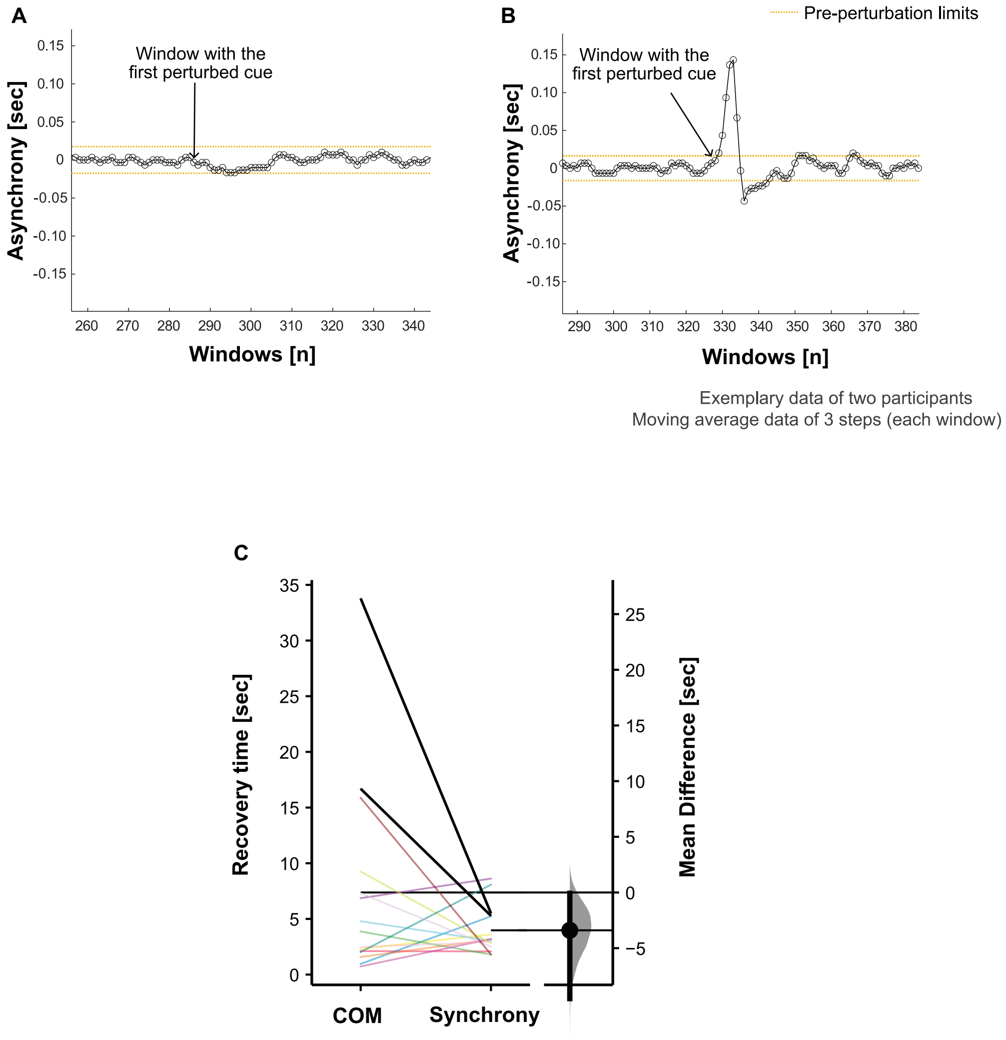
Perturbation magnitude: 20× SD of Step time. Perturbation time: total time for the five perturbed cues, 5× Mean + 20× SD of Step time. SD, standard deviation; COM, center of mass; CW, cued walking; BW, baseline walking; CI, confidence intervals.

In two of the five participants who did not show deviation from steady state, there was no noticeable adjustment of the step time to achieve the alignment of the footsteps with the perturbed cues. The remaining three exhibited no measurable COM deviation from steady state patterns despite synchronizing to the perturbed cues.

In the evaluation of footfall timing adaption to recover synchronization with the beat, the average synchrony recovery time was 4.0 (2.1) s. Overall, the differences in recovery time for COM kinematics relative to footfall synchrony was +3.4 [95.0% CI +0.1, +9.5] s (**Figure 3C**). However, 7 out of the 15 participants recovered the COM kinematics ahead of the recovery of footfall synchrony.

Comparison of Vector Counts Between Trials

The reconstructed COM trajectory was outside $T_{3\sigma}$ on average for 16.8% of CW_2 (period from onset of auditory perturbation until COM recovery) in comparison to <1% for the rest of the trial (CW_1 and CW_3, **Figures 4A,B**). The differences between CW and



Exemplary data of two participants
Moving average data of 3 steps (each window)

Data from N=15 participants labelled in different colours

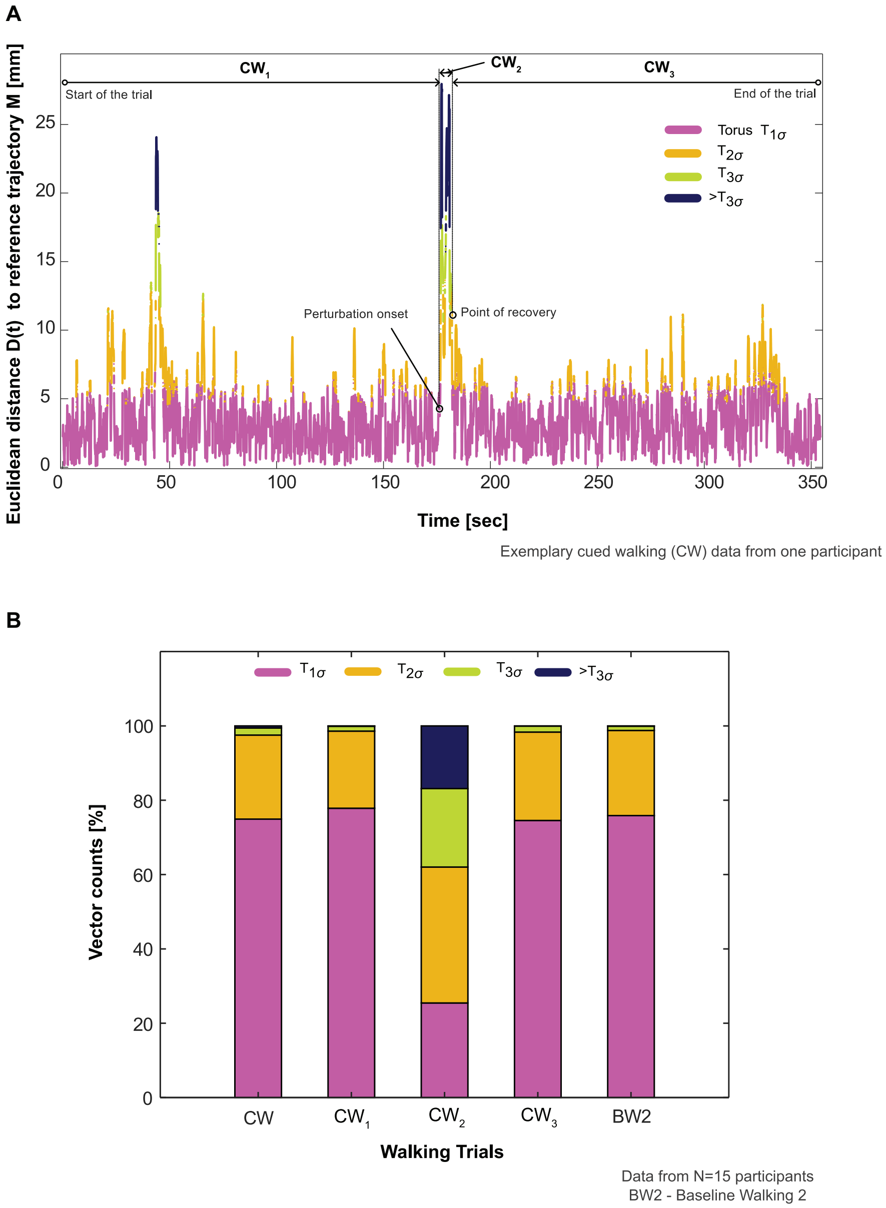
The mean difference together with confidence intervals are displayed (as a point estimate and vertical bar respectively)

FIGURE 3 | Footfall asynchrony characteristics. Adjustment of step time to align the footsteps with perturbed cues (i.e., synchronization) was achieved in 18 out of 20 participants. Exemplary data are presented to demonstrate the asynchrony (refer to section "Recovery of Footfall Synchrony to Pre-perturbation Limits" in the manuscript for calculation details) characteristics in panel **(A)** a participant who did not adjust their step time to achieve the alignment of the footsteps with the perturbed cues and **(B)** a participant who did synchronize to the perturbed auditory cues. **(C)** Comparison of center of mass (COM) and synchrony recovery times in all the participants who showed deviation from steady state patterns in response to the auditory perturbation (*N* = 15).

BW2 were $T_{1\sigma}: -0.9\%$; $T_{2\sigma}: -0.9\%$; $T_{3\sigma}: +0.8\%$; $> T_{3\sigma}: +0.5\%$, **Table 1**.

DISCUSSION

The pilot study was designed to investigate whether and how rhythmic auditory perturbations in a sensorimotor synchronization paradigm influence the dynamic stability of walking. This aim was achieved by subjecting 20 healthy young adults to a beat delayed perturbation in a metronome sequence to manipulate their footfall rhythmicity and characterize the resulting COM kinematics. Our results show that in all but five participants, the imposed perturbation modified each individual's walking rhythm and resulted in COM deviations (average maximum deviation of ∼28 mm) away from steady state patterns. In response to the perturbation, the mean COM recovery time across all participants who showed deviation from steady state ($N = 15$) was 7.4 s (equivalent to approx. 12 steps). Importantly, recovery of footfall synchronization with the metronome beats after perturbation was achieved more rapidly (by 3.4 s) on average compared to COM kinematics. In



Exemplary cued walking (CW) data from one participant

Data from N=15 participants
BW2 - Baseline Walking 2

FIGURE 4 | Participants' aggregate response to the auditory perturbation. **(A)** Comparison of an exemplary participant's aggregate response in the cued walking (CW) trial during the period of recovery (CW$_2$, onset of auditory perturbation until center of mass recovery) to before (CW$_1$, start of the walking trial until the onset of the perturbation) and after this period (CW$_3$, point of center of mass recovery until the end of the trial). The proportion of vector counts within the steady state boundaries (Torus $T_{1\sigma}$, $T_{2\sigma}$, $T_{3\sigma}$) and outside ($>T_{3\sigma}$) determined the aggregate response. **(B)** Comparison of participants' aggregate response between the different phases of CW, CW itself, and baseline walking 2 (BW2) in all the participants who showed deviation from steady state patterns in response to the auditory perturbation (*N* = 15).

conclusion, the quantification of an individual's COM recovery time to steady-state movement patterns after rhythmic auditory perturbations has showcased an experimental framework for assessing an individual's resilience to rhythm perturbations, and potentially also their fall risk.

Previous studies have shown that synchronizing movement with metronome beats may not be automatic and require some attention and volition (Repp and Keller, 2004; Miyake, 2009; Peper et al., 2012; Terrier and Deriaz, 2013; Mendonca et al., 2014; Hove and Keller, 2015; Leow et al., 2018; Moumdjian et al., 2019). In this respect, metronome beats seem to draw participants' attention toward the target event in the movement (e.g., footfall) timing, thereby making walking less automatic (Repp, 2005; Peper et al., 2012). This suggests that guided stepping with external auditory cues may require additional frontoparietal structures to be engaged, including networks responsible for attention, e.g., the prefrontal cortex (Wagner et al., 2016, 2019). Interestingly, it has previously been demonstrated that higher attentional demands to perceive a beat and accurately synchronize movement does not negatively influence overall walking stability and balance performance (Nanhoe-Mahabier et al., 2012; Terrier and Deriaz, 2013). Yet this finding does not rule out the risk of instability due to the adjustment of footfall timing at instances when deviations from synchrony occur (naturally: e.g., participants lose attention, desynchronize and attempt to resynchronize, or experimentally: perturbations similar to those imposed in the current study). In line with these expectations, our study substantiates the hypothesis that rhythmic auditory perturbations are able to alter an individual's stable movement patterns. Here, we observed large inter-individual variability in the maximum deviation (SD: 13.5 mm) and recovery time (SD: 8.9 s) of COM kinematics to relatively small differences in the perturbed time (SD: 0.5 s).

Two participants did not adjust their step time to achieve the alignment of the footsteps with the perturbed cues. It seems that these participants consciously followed and maintained the rhythmic cues before perturbation and not adapted to the variations. Three participants maintained a consistent COM movement pattern within steady state boundaries, despite modifying their footfall rhythm to perturbations. While we cannot be exactly sure how these individuals were able to maintain stable COM kinematics, we would argue that it involves prioritization of different balance strategies or flexible vs. rigid movement responses. On the neurophysiological side, these participants may have allocated less attentional resources toward synchronization (and used the internal cueing from basal ganglia) and more toward the maintenance of balance. Ensuring motor actions in time with perturbed cues may require attention and error-correction processes. The neural mechanisms underlying these processes are continuing to be debated. Neuroimaging studies have linked them to a broader network of brain areas including the auditory cortex, basal ganglia, cerebellum, pre-motor, and **Supplementary Motor Areas** (Grahn and Brett, 2007; for a review, see also Koshimori and Thaut, 2018; Damm et al., 2020). Further, a recent electrophysiological study suggest signatures of step adaptation to auditory perturbations in the cortical beta activity: beta band supression in the central and parietal cortex and an increase of beta power in the prefrontal regions (Wagner et al., 2016). The authors suggest that the former may be involved in the readiness and voluntary execution of movements and the latter may allow the cognitive flexibility to adapt the movements. And in so doing, these research promises to enrich our understanding of the neural mechanisms underlying movement adaptation to auditory perturbations.

Prior research advocates a close connection between the process of synchronization correction and maintaining stable movement patterns during adaptation to rhythm perturbations (Chen et al., 2006; Wright et al., 2014; Hove and Keller, 2015). When a perturbation occurs in the auditory sequence, a subject's behavioral response to restore synchrony with the cues may be constrained by the position of their COM relative to their feet to maintain balance and prevent falling. In the present study, we additionally tested whether the participants prioritized the recovery of COM kinematics over footfall synchronization after perturbation. However, we found no substantial evidence for this expectation, i.e., no significant differences between COM and synchrony recovery times. A caveat of these findings may be the young and healthy composition of our cohort, as it has been shown that such subjects may not be as susceptible to dual-tasking interference as older adults and clinical populations (Brauer et al., 2001, 2002). Here, older populations might prioritize COM kinematics over task synchrony in order to reduce their propensity to fall (Bleom et al., 2006). While these issues remain to be elucidated in future studies, the findings may have important implications regarding task prioritization in real-life walking scenarios.

Neural feedback mechanisms for sensing and responding to rhythm perturbations naturally involve latencies (Wagner et al., 2019; Zhang et al., 2020). When combined with timing constraints to integrate information from sensory and motor systems in higher brain centers for movement planning and execution, such latencies may be critical for the recovery time of movement to perturbations (Repp and Su, 2013; Hove et al., 2014; Daley, 2018; Koshimori and Thaut, 2018). Our previous experimental work (Ravi et al., 2021) and the results from the current study have largely detailed how humans recover COM kinematics (i.e., resilience) gradually to steady-state patterns in subsequent steps after perturbation. One might ask, therefore, whether individuals are unstable during the apparently long period of recovery. To elucidate this, we analyzed each participant's COM trajectory composition within different steady state boundaries and found that movement patterns during the period of recovery (CW_2, **Figure 4A**) exhibited a noticeable proportion of time outside $T_{3\sigma}$ (16%, **Figure 4B**) in comparison to other phases of CW.

The magnitude of perturbations to the auditory stimuli used in the majority of published literature to date has been selected somewhat arbitrarily and discordantly: phase shifts of 50 ms (Chen et al., 2006); 60° (Roerdink et al., 2009; Nijs et al., 2020); 100 ms (Wright et al., 2014); and 15% of step cycle (Khan et al., 2020). In the present study, we perturbed the metronome cues based on each individual's step time variability (measured in standard deviations). This approach is arguably less susceptible to participant bias due to its insight into each individual's walking performance, rather than at arbitrarily chosen levels. However, further study should be carried out to investigate the advantages and disadvantages of this approach. Future work must also address the differences in COM recovery time between lengthening (as used in the current study) and shortening the IBI of the perturbed cues. Encouragingly, there is previous evidence that participants make larger footfall corrections (that could incur larger instability) when the perturbation IBIs are shortened as opposed to lengthening the intervals (Wright et al., 2014).

It has been suggested that individuals rely on cycle-to-cycle corrections to maintain coordination with an auditory stimulus (Vaz et al., 2019). As such, studies typically analyze only discrete events in the walking cycle (e.g., heel contact), but corrective adjustments are likely to occur continuously throughout different phases of a gait cycle. Here, the analysis of footfall synchrony recovery time could be further extended to characterize the distribution of timing correction across a walking cycle. When combined with our analyses to quantify resilience to perturbations, such approaches provide a valuable insight into gait phase-specific variation in balance response and its interaction with external sensory cues and perturbations. Moreover, these approaches could lay the foundations for understanding rhythm deficits in neuromotor pathologies and rehabilitation, and thereby support clinical decision making.

A number of limitations of this pilot investigation should be acknowledged. First, our experimental protocol was limited to recording only a few body segments. Notably, we could not determine the body's actual COM, but rather used only an approximation based on the sacral marker. Additionally, it was not possible to provide a characterization of upper body rhythmic movement response (i.e., timing of arm swing or head bobbing) to auditory stimulation and perturbation. Second, we did not collect subjective feedback about the experiment. In this study, two participants missed the perturbed cues, despite prior instruction to synchronize to the auditory cues. While this was unexpected, post-experiment feedback would have allowed us to better understand whether these participants perceived the perturbation in the auditory cues or misunderstood the instructions. Third, while the minimum number of dimensions required to form properly a state-space of the COM was evaluated to be 4, we used only three dimensions in the current study. This is a limitation of our 3D torus-based approach but the sensitivity of our findings to such differences need further exploration. Fourth, we could not align the audio track and motion capture data in the time axis, because we failed to account a temporal delay in one of the data streams. However, this temporal delay did not affect the analyses and results of the present study.

In summary, locomotion in complex, dynamic real-world environments is an integral part of daily life of humans. While walking in such environments, individuals modulate their footfall timing and rhythmicity to maintain the body's COM, which is a critical factor in their successful and continuous ambulation (i.e., fall avoidance). The present study extended the sensorimotor synchronization paradigm to include analysis of COM recovery time and has provided a novel framework for improving our understanding of an individual's resilience to perturbations. It also provides a starting point in the use of these techniques toward understanding an individual's ability to avoid falls. At a fundamental level, we show not only differences between COM and synchrony recovery times, but that even young adults took up to 12 steps to recover stable movement patterns from a relatively innocuous perturbation.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation. The codes to reproduce the central findings in this study (COM recovery time after auditory perturbations) is publicly available at: https://github.com/laboratory-of-movement-biomechanics-eth/locomotor-resilience.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by ETH Zürich Ethics Commission. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

DR and CH conceived and designed the study. NS and WT supervised the project and provided critical opinions as subject experts. CH performed the data collection. DR and CH did the subsequent data analysis. DR, WT, and NS drafted the manuscript. WT is the guarantor. All the authors reviewed and approved the final manuscript for submission.

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SUPPLEMENTARY MATERIAL

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BRIEF RESEARCH REPORT
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Tapping to Music Predicts Literacy Skills of First-Grade Children

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The ability to synchronise one's movements to the sound of a regular beat has been found to be associated with children's language and reading abilities. Sensorimotor synchronisation or tapping performance can among other factors [e.g., working memory and rapid automatized naming (RAN)] predict phonological awareness and word reading accuracy and fluency of first graders. While tapping tasks that use a simple metronome sound are more often used, applying musical stimuli has the potential advantage of being more engaging and motivating for children. In the present study, we investigated whether tapping to a metronome beat or complex musical stimuli would predict phonological awareness and reading outcomes of Hungarian 6-7-year olds ($N=37$). We also measured participants' general cognitive abilities (RAN, non-verbal intelligence and verbal working memory). Our results show that phonological awareness, spelling and reading accuracy were associated with the musical tasks while reading fluency was predicted by the metronome trials. Our findings suggest that complex musical tasks should be considered when investigating this age group, as they were, in general, more effective in predicting literacy outcomes.

Keywords: sensorimotor synchronisation, tapping, rhythm, reading fluency, reading accuracy, phonological awareness

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INTRODUCTION

Moving together with the rhythm of music is a human universal (Nettl, 2000) that has been associated with the use of vocal learning and communication (Patel et al., 2009). There is also mounting evidence linking non-linguistic rhythmic abilities to literacy and reading-related cognitive skills (e.g., Moritz et al., 2013; Gordon et al., 2015; Patscheke et al., 2019). In the present study, we investigated whether a specific rhythmic ability that is synchronising one's tapping to a steady beat could predict 6-7-year-olds' literacy. We also compared the effectiveness of two different kinds of stimuli: the more widely used, simple metronome clicks and complex music that provides higher ecological validity.

A substantial body of research has explored the possible role of rhythmic skills in addition to well-established predictors of early literacy, such as short-term verbal memory (Peng et al., 2018), rapid automatized naming (RAN; Kirby et al., 2003) and phonological awareness (Goswami, 2018). Rhythmical skills have been associated with language and literacy investigating individuals with typical (David et al., 2007; Gordon et al., 2015; Bonacina et al., 2018; Politimou et al., 2019) and atypical language development, specifically developmental dyslexia (Flaugnacco et al., 2014; Woodruff Carr et al., 2014; Flaugnacco et al., 2015; Colling et al., 2017) and specific language impairment (Alcock et al., 2000; Corriveau and Goswami, 2009; Cumming et al., 2015).

Although there seems to be solid evidence linking rhythmic skills to reading acquisition, it is not yet clear what mediates this relationship. In their meta-analysis, Ozernov-Palchik and Patel (2018) have found that performance in especially beat-based rhythmic tasks was associated with children's reading performance and proposed that the ability to extract regularities from an auditory stream and make predictions based on them would be the link between rhythmic abilities and phonological awareness. In the authors' view, phonological awareness would serve as a mediator between the two domains. With similar reasoning, the Precise Auditory Timing Hypothesis (Tierney and Kraus, 2014) emphasises that both phonological skills and the ability to synchronise to a beat rely on precise neural timing and suggests that the rhythm-reading link is established through the mediation of phonology. Synchronisation on a behavioural level is widely measured using the sensorimotor synchronisation task (SMS; Repp, 2005; Repp and Su, 2013) commonly referred to as tapping to a beat.

Indeed SMS or tapping performance has been found to predict reading outcomes of Norwegian first graders (Lundetræ and Thomson, 2018) rise time perception and reading of 8-11-year-old Italian students (Flaugnacco et al., 2014), phonological processing, RAN, word reading and spelling among English speaking American 5-7-year olds (Bonacina et al., 2018) and French third graders (Lê et al., 2020). In the latter, tapping performance was not only associated with literacy scores through the mediation of phonological awareness but also showed a direct effect in the applied SEM analysis.

Building on evidence from studies with individuals with developmental dyslexia, the Temporal-Sampling Theory proposes an auditory perception framework. According to which impaired temporal processing of speech, results in imprecise phonological representations that lead to atypical reading, while the same deficit reveals itself in impaired beat processing often observed among individuals with dyslexia (Goswami, 2018). Congruent with TST, dyslexic children and adults (Wolff, 2002; Flaugnacco et al., 2014; Colling et al., 2017) and those with specific language impairment (Corriveau and Goswami, 2009; Cumming et al., 2015) have been found to be less able to synchronise to a beat.

Tapping to music, as opposed to more commonly used simple metronome clicks, has the potential benefit of engaging children more and sustaining their motivation. However, the number of studies with children using musical stimuli is scarce. In a study (Cumming et al., 2015), 9-year-old children's tapping to music remained a significant predictor of SLI diagnosis after controlling for IQ. Although their results show that a musical task can be effective in identifying individual differences, comparison of the two stimuli was not possible due to the lack of a metronome task. Some insight may be gained from an investigation of children diagnosed with ADHD (Puyjarinet et al., 2017). When 6-12-year-old participants were asked to tap along with excerpts of classical music, their synchronisation performance deteriorated significantly compared to the metronome task. We cannot however infer that stimulus complexity has a generally negative effect on tapping performance as it could be attributable to attention deficits characteristic of ADHD. A study with contrasting results (Einarson and Trainor, 2016) compared typical developing children's tapping to music and metronome and found that 5-7-year olds were able to synchronise their taps better when listening to music compared to metronome sound in the same tempo. A feasible explanation would be that contrary to their peers with ADHD, typical developing children can take advantage of the rhythmic complexity of music and use the richness of rhythmic cues to make temporal predictions.

In this present study, we aimed to investigate whether a musical or a metronome tapping task would be more successful in predicting children's language and reading skills, and how stimulus complexity influences tapping performance. Based on previous studies, we hypothesised that the musical tasks would help children to synchronise to the beat resulting in more precise tapping. We could not, however, make any valid assumptions on which task would be more successful in predicting language and reading scores due to the lack of similar investigations in the literature.

MATERIALS AND METHODS

Participants

Thirty-seven typically developing first-grade children from the Németh Imre Primary School, Budapest, Hungary took part in the current study (mean age = 7.4; *SD* = 0.4; 18 girls, 19 boys). All came from families that spoke Hungarian as a first language. None of them had any known neurological disorders, learning or hearing disabilities. Parents gave their written consent after being informed about the procedure. Children were also informed previously in the classroom and at the beginning of the testing sessions about the tasks and their right to withdraw their consent at any time. The study was approved by the Research Ethics Committee of Eötvös Loránd University Faculty of Education and Psychology.

Equipment

Children were asked to tap along on an AKAI LPD8 MIDI controller, listening to music or a metronome through Audio-Technica ATH-T200 headphones, connected to a computer through a Steinberg U-22 interface. Steinberg Cubase 5 was used for playback and recording taps.

Measurements

Tapping Tasks

Children were given two tapping tasks, tapping to music in three tempi (80, 120 and 150 bpm) and tapping to a metronome also in the same tempi (80, 120 and 150 bpm). The six trials were administered in a pseudo-random order. We used the synchronisation-continuation design in which participants were required to keep on tapping after the auditory stimulus has stopped. Children were given a short demonstration of the task which only started once they understood what they were expected to do. If a participant misunderstood the task or used an atypical strategy (e.g., tapping in antiphase or double time) they were asked to start again after a second demonstration and clarification.

Tapping to Music

In the musical tasks, children were instructed to listen to four quarter notes as a count-in at the beginning of each trial, then tap along with the music and continue so even after the music has ended until asked to stop. The synchronisation phase or paced tapping lasted for approximately 30 s corresponding to the particular piece of music being played. In the continuation or unpaced tapping phase, participants were asked to keep tapping in the same tempo until being asked to stop (another 30 s). To give participants an unambiguous sense of beat and avoid additional cues due to familiarity with the particular song, popular musical pieces were selected that are mostly unknown to Hungarian children. We also considered pop music a good choice because even though participants are not familiar with the songs themselves, the simple rhythmic and melodic motives are known to them through enculturation. Instrumental versions of three popular songs were created for the study: Dream, dream, dream (Everly Brothers), Michelle (The Beatles) and Johnny B Goode (Chuck Berry). All three were rendered from MIDI score using virtual instruments with the same instrumentation to avoid timbral differences. Vocal melody parts were removed to not give an advantage to those who were familiar with the particular song. Participants were asked if they were familiar with the particular pieces, but none of them could identify any of the songs.

Tapping to Metronome

Stimuli for the metronome trials were created with the same tempo and length as in the musical trials of the corresponding tempo, including the end of the synchronisation phase. For metronome sound, a woodblock sample was used from the Cubase5 library. Identical measures were calculated for the musical trials: synchronisation accuracy, synchronisation and continuation tapping consistency.

Synchronisation Phase

The first 10 taps were discarded from the analysis. Rayleigh's tests were calculated to exclude trials in which tapping did not significantly differ from random distribution. ITIs (inter-tap intervals) for each trial were gathered for all participants to identify outliers. ITIs greater than the third quartile + three times the interquartile range (Q3 + 3*IQR) or smaller than the first quartile – three times the interquartile range (Q1–3*IQR) were considered outliers and were removed. After calculating the difference between each tap and the nearest target beat, two data analysis methods were applied. To measure tapping accuracy, the mean of the absolute values of differences was divided by the tempo of the music, resulting in a variable showing the deviation from the reference as a percentage, where a value of 0 means total synchrony with the stimulus. To calculate tapping consistency, circular statistical analysis was applied. Circular statistics is commonly used with cyclical or directional data (e.g., Falk et al., 2015). Individual tapping asynchronies were transformed as points on the circumference of a unit circle, representing the distance from the nearest target beat, where 0° means a perfectly timed tap. For example, in a 500 ms tempo trial, a tap following the beat by 125 ms would be represented by a unit vector at 90°, while the beat preceding by 125 ms at −90°. The length of the resultant vector (R) averaged from the unit vectors, reflects the variability of the participant's taps in the given trial. We used R vector length as a measure of tapping consistency, a value between 0 and 1, 0 meaning complete inconsistency and 1 meaning perfect consistency (**Figure 1**).

Continuation Phase

The continuation phase consisted of 30 s of unpaced tapping immediately following the synchronisation phase. Only the first 30 taps were analysed and trials of less than 10 taps were excluded. Because of the lack of reference in this phase, circular statistics could not be applied. Tapping consistency was calculated as 1 – CV (coefficient of variance) of the ITIs, 1 meaning a hypothetical level of total consistency.

General Cognitive Abilities

To assess their cognitive abilities, students were administered three subtests from the fourth edition of the Wechsler Intelligence Scale for Children (Wechsler, 2003; Nagyné Réz et al., 2008): Block Design, Digit Span and Vocabulary. Age-specific standard scores were calculated and used in later analyses. The Block Design subtest was used to measure non-verbal reasoning and visuospatial abilities. Children were asked to assemble patterns presented to them on a coloured sheet, using red and white painted cubes within a given time limit. The Digit Span subtest, a measurement of verbal working memory, consisted of trials of progressively lengthening sequences of digits that children had to repeat in identical or in reverse order. Scores were calculated from the length of the longest forward and backward sequences successfully reproduced. Finally, in the Vocabulary subtest, students were asked to describe 36 words in their own way. Scores were calculated by the adequacy of their definitions using the WISC-IV manual.

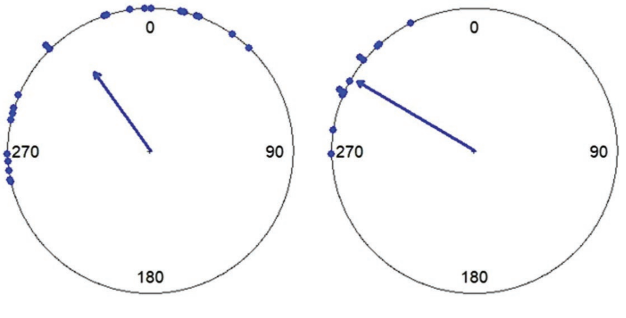

FIGURE 1 | Circular plots of an individual's tapping in two trials. Dots show single taps while the arrow represents the resultant vector. In the first case (left), taps are more consistent, shown by the arrow's length and the mean angle signifies anticipation looking at its direction. In the second case (right), taps are less consistent while the vector's direction shows a higher accuracy.

Reading and Language Tests

Four subtests were selected from the Dyslexia Differential Diagnosis, Maastricht, Hungarian adaptation (3DM-H; Blomert and Vaessen, 2009; Tóth et al., 2014). In the Reading subtest, children were presented low- and high-frequency words and pseudowords on the computer screen. Blocks were 30 s long; students were required to read as many words as possible. The length of the words and pseudowords increase gradually. Performance was assessed by fluency (how many words children were able to read) and precision (the ratio of correct answers). The Phoneme Deletion subtest required children to listen to 27 pseudowords of gradually growing complexity and repeat them excluding a certain phoneme. The percentage of correct answers was used as the measure of accuracy. In the Spelling subtest, participants were presented words through the headphones and simultaneously on the computer screen with a missing letter. They were required to complete the words using four colour coded possibilities. The percentage of correct answers was used as a measure of their performance. The Rapid Automatized Naming subtest required students to name 2 × 3 blocks of letters, numbers and pictures as quickly as possible. The performance was measured by the time used for completing a block. All measurements from the 3DM-H test are given as z-score in the analysis.

Procedure

Children were assessed individually in two sessions, planned to take part in March of 2020. Students were administered the three tapping tasks and the three subtests from WISC-IV in a quiet, separate room. This first session (including the tapping tasks and WISC-IV) lasted approximately 40 min. Participants completed reading and language tests (3DM-H) in the second session which lasted for an average of 30 min. Due to the COVID-19 epidemic, the second session had to be delayed until September of 2020, the beginning of the second school year.

Data Analysis

Data analysis was carried out using IBM SPSS Statistics, Version 23 (IBM Corp., 2015), JASP (Version 0.13.1; JASP Team, 2020) and R Studio (R Core Team, 2020). Outlier values below Q1-1,5*IQR or above Q3 + 1,5*IQR were identified and removed from each variable using boxplots. Paced and unpaced tapping were analysed separately. Overall tapping measurements were calculated for metronome and musical trials as the mean of the three different tempo trials resulting in six variables in total: Paced musical asynchrony, Paced metronome asynchrony, Paced musical consistency, Paced metronome consistency, Unpaced musical consistency and Unpaced metronome consistency. To compare tapping performance across musical and metronome trials, paired-sample t-tests were carried out. The assumptions of normality were tested using the Shapiro–Wilk method. The relations between tapping measurements, WISC-IV and RAN scores and reading and language outcomes were explored by building multiple linear regression models using the stepwise method. Variables were automatically entered when the value of p was equal to or lower than 0.05 and removed when above or equal to 0.10. A post-hoc power analysis was conducted using the GPower software package (Faul et al., 2007), indicating that while statistical power was more than adequate for the first two models (0.95 and 0.83), the third and fourth models showed lower levels (0.66 and 0.71) which highlight the limits of interpretation of the latter two (for parameters, see **Supplementary Material**).

RESULTS

Differences Between Tapping to Metronome and Music

Descriptive statistics for the observed measures is shown in **Table 1**. To compare the tapping performance to metronome and music, paired-samples *t*-tests were conducted for variables paced tapping asynchrony, paced tapping consistency and unpaced tapping consistency. Normality assumptions were assessed using the Shapiro–Wilk test. For paced tapping consistency, there was a significant difference in the scores for musical (M = 0.76, SD = 0.16) and metronome ($M = 0.83$, $SD = 0.09$) conditions $t(30) = -2.59$, $p = 0.015$; $d = -0.47$. Children tapped with higher consistency when listening to metronome sound compared to music. A significant difference was found for paced tapping asynchrony between musical ($M = 0.91$, $SD = 0.06$) and metronome ($M = 0.92$, $SD = 0.05$) conditions $t(33) = 3.02$, $p = 0.005$; $d = -0.52$. Participants were able to synchronise their tapping with lower asynchrony to music than to metronome. For continuation tapping consistency, there was a significant difference in performance for musical ($M = 0.09$, $SD = 0.02$) and metronome ($M = 0.08$, $SD = 0.05$) conditions $t(32) = -3.47$, $p = 0.002$; $d = -0.60$. Tapping inconsistency was lower for continuation tapping following metronome than for music.

TABLE 1 | Descriptive statistics for all observed measures.

Tests	*M* (*SD*)	
Spelling	−0.94	(0.63)
Phonological awareness	−0.74	(0.82)
Reading fluency	2.28	(1.00)
Reading precision	0.89	(0.09)
RAN	1.38	(0.19)
Digit span	11.06	(2.14)
Block Design	12.03	(3.48)
Vocabulary	14.68	(3.01)
Tapping consistency – music	0.76	(0.16)
Tapping consistency – metronome	0.83	(0.08)
Tapping asynchrony – music	0.12	(0.06)
Tapping asynchrony – metronome	0.15	(0.05)
Continuation consistency – music	0.91	(0.02)
Continuation consistency – metronome	0.92	(0.01)

The Relation Between Tapping Performance, Reading and Language Scores

To predict reading and language outcomes (Phoneme deletion, Reading fluency, Reading precision and Spelling), tapping variables for musical and metronome trials (Paced tapping consistency, Unpaced tapping consistency and Paced tapping accuracy), WISC-IV subtest scores (Vocabulary, Digit span and Block design) and RAN performance were entered in a series of multiple linear regression analyses using the stepwise method. The coefficients of the described linear models are summarised in **Table 2** and visually represented in **Figure 2**. For Phoneme deletion, a significant model was found $F(1, 28) = 11.07$, $p = 0.002$, $R^2 = 0.28$, R^2 Adjusted $= 0.26$ in which Paced musical tapping consistency ($t = 3{,}327$, $p = 0.002$) was the only significant predictor (**Table 2**) although Block design scores almost reached the limit of significance ($p = 0.066$) of inclusion in the model. The relationship between Phoneme deletion and Paced musical tapping consistency is shown in **Figure 2**. An analysis of standard residuals was carried out, which showed that the data contained no outliers (Std. Residual Min = −2.12, Std. Residual Max = 1.91). The assumption of independent errors was met (Durbin-Watson value = 2.26). The histogram of standardised residuals indicated that the distribution of errors was approximately normal, as did the P–P plot of standardised residuals, showing points that were not exactly on the line, but acceptably close. Looking at the scatterplot of standardised predicted values, we found that the data met the assumptions of homogeneity of variance and linearity. The assumption of non-zero variances was also met (Paced musical consistency, Variance = 0.02; Phoneme deletion, Variance = 0.67).

Spelling was best predicted by a model $F(1, 28) = 7.07$, $p = 0.013$, $R^2 = 0.20$, $R^2_{\text{Adjusted}} = 0.17$ with Paced musical asynchrony ($t = -2.66$, $p = 0.013$) as the independent variable. The analysis of standard residuals showed that the data contained no outliers (Std. Residual Min = −2.48, Std. Residual Max = 2.50) and met the assumption of independent errors (Durbin-Watson value = 2.65). Examining the histogram of standardised residuals, an approximately normal distribution of errors was found. The P–P plot of standardised residuals showed an acceptable deviation from the line. The scatterplot of standardised predicted values showed that the data met the assumptions of homogeneity of variance and linearity. The assumption of non-zero variances was met (Paced musical asynchrony, Variance = 0.003; Spelling, Variance = 0.39).

A significant model was found $F(1, 28) = 5.23$, $p = 0.030$ with $R^2 = 0.16$, $R^2_{\text{Adjusted}} = 0.13$ to predict reading fluency with the single variable Paced metronome consistency ($t = 2.29$, $p = 0.030$). Analysing standard residuals we found that the data did not contain any outliers (Std. Residual Min = −1.80, Std. Residual Max = 1.97). The assumption of independent errors was met (Durbin-Watson value = 2.35). We found an acceptably normal distribution of errors looking at the histogram and the P–P plot of standardised residuals. The scatterplot of standardised predicted values indicated that the assumptions of homogeneity of variance and linearity were not violated. The variances of the variables in the model indicated that

TABLE 2 | Regression coefficients of the final models for phoneme deletion, spelling, reading fluency and reading accuracy.

Variable	Phoneme deletion				Spelling				Reading fluency				Reading accuracy		
	B	**β**	**SE**		**B**	**β**	**SE**		**B**	**β**	**SE**		**B**	**β**	**SE**
Constant	-2.88^{**}		0.66	Constant	−0.34	0.25		Constant	−1.58	1.69		Constant	0.72^{**}	0.08	
Tapping consistency (music)	2.81^{**}	0.53	0.85	Tapping asynchrony (music)	-4.96^{*}	1.87	−0.45	Tapping consistency (metronome)	4.66	2.04	0.40	Tapping consistency (music)	0.23^{*}	0.10	0.40
R^2	0.28^{**}			R^2	0.20^{*}			R^2	0.16			R^2	0.16^{*}		

$^{*}p<0.05$; $^{**}p<0.01$

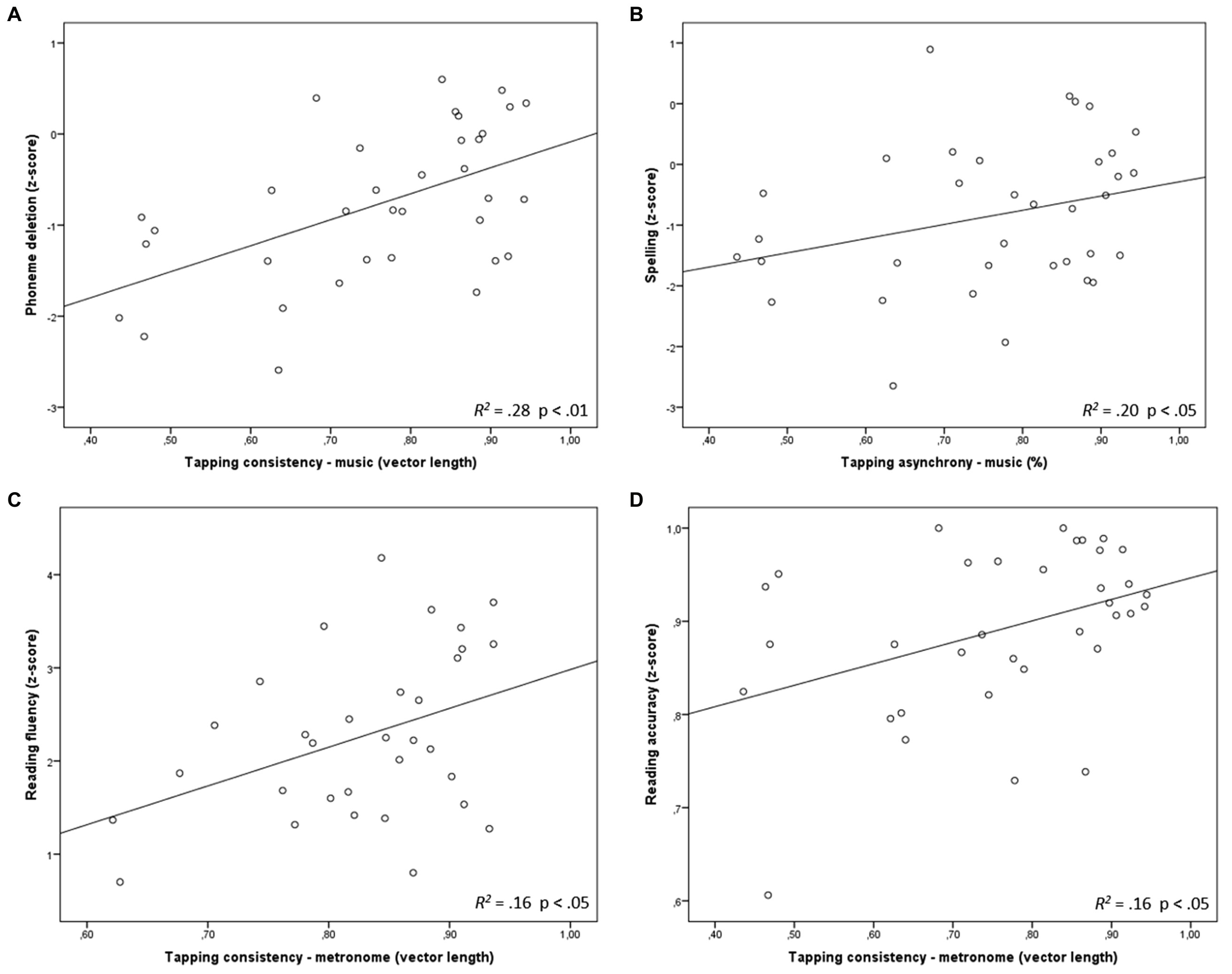

FIGURE 2 | Relation between tapping consistency in musical tasks and phoneme deletion **(A)**, tapping asynchrony in musical tasks and spelling **(B)**, tapping consistency in metronome tasks and reading fluency **(C)** and tapping consistency in metronome tasks and reading accuracy **(D)**. Consistency is given as the length of the resultant vector (see Measurements), where 1 stands for perfect consistency and 0 for inconsistency. Tapping asynchrony is given as the mean asynchrony of the taps (see Measurements), where 1 represents total synchrony and 0 asynchrony.

the assumption of non-zero variances was also met (Paced metronome consistency, Variance = 0.007; Reading fluency, Variance = 0.99).

A significant regression model was found $F(1, 28) = 5.38$, $p = 0.03$, $R^2 = 0.16$, $R^2_{\text{Adjusted}} = 0.13$ in which Paced musical consistency ($t = 2.32$, $p = 0.03$) predicted Reading precision scores. An analysis of standard residuals showed that the data were free of outliers (Std. Residual Min = −2.72, Std. Residual Max = 1.53). The assumption of independent errors was met (Durbin-Watson value = 2.50). The histogram and P–P plot of standardised residuals showed approximately normally distributed errors. The scatterplot of standardised predicted values indicated that the assumptions of homogeneity of variance and linearity were not violated. The assumption of non-zero variances was also met (Paced musical consistency, Variance = 0.024; Reading precision, Variance = 0.008).

DISCUSSION

In our present study, we investigated the relationship between Hungarian first graders' ability to tap to a beat and their literacy development, and we also studied the difference between tapping to music and tapping to a metronome. By building linear models using the stepwise method, we found that measures of tapping performance were successful in predicting literacy scores. Paced tapping consistency in musical tasks accounted for 28% of the variance in phoneme deletion and 13% in reading precision scores. Spelling was best predicted (17%) by absolute asynchrony in paced tapping in musical tasks while reading fluency by tapping consistency in paced metronome tasks (13%). Surprisingly none of the additional predictors, such as RAN, verbal working memory, vocabulary or non-verbal intelligence, were contributing significantly to the final models. We found that musical tasks were more successful in predicting language and reading scores except for reading fluency. A possible interpretation is that those children who were able to extract the beat from the musical stimuli, thus taking advantage of its higher complexity also have an advantage in extracting regularities from speech. This would be congruent with the framework of Ozernov-Palchik and Patel (2018). Our findings are also consistent with PATH framework (Tierney and Kraus, 2014) as phonological awareness was best predicted by tapping consistency. Unpaced tapping consistency, however, did not improve any of the models as we would have expected based on findings of Maróti et al. (2019). Unpaced tapping variability was altogether found to be low in our sample. A possible explanation is that children develop the capability to keep a steady beat earlier than being able to synchronise their taps to an external beat (Provasi and Bobin-Bègue, 2003; Zentner and Eerola, 2010; Provasi et al., 2014). As unpaced compared to paced tapping does not include error correction, the ability to monitor, perceive and correct one's asynchrony might also be a key feature in predicting literacy.

Comparing children's performance in musical and metronome tasks, we found that paced and unpaced tapping consistency was higher for metronome trials, while asynchrony was lower when tapping along with music. These findings are congruent with those of Einarson and Trainor (2016) who also found more consistent tapping but lower phase alignment for metronome trials. Similar findings were reported (Dalla Bella et al., 2017) with adults whose taps showed higher accuracy for musical trials compared to those with a metronome beat. The authors explain their findings with the well-documented phenomenon called Negative Mean Asynchrony which is the tendency for taps to precede the target beat. Although there are contrasting findings in the literature this anticipatory behaviour was found to disappear when listening to stimuli with higher rhythmical complexity (Repp, 2005; Repp and Su, 2013). Our findings suggest that musical tasks in which children have to synchronise to more complex stimuli might tap into some underlying mechanism also involved in language and reading acquisition, for example, statistical learning or executive functioning. Another important remaining question is whether indeed tapping performance predicts reading outcomes through phonological awareness or directly as in the study of Lê et al. (2020).

It should be considered that our results come from a relatively small sample which not only led to lower levels of significance in the statistical analysis but also altogether limits the generalizability of our findings. Furthermore, as mentioned before testing sessions were conducted several months apart due to the COVID-19 pandemic, making our findings somewhat less cross-sectional in nature. Furthermore, the musical stimuli of the present study represent a small proportion of styles, which might limit its generalizability. Future research might benefit from including a wider spectrum of genres. These first preliminary findings of our ongoing research raise important future issues, for example, of the role of such predictors as RAN or verbal working memory which did not account for unique variance of reading and language skills in this study.

Our current findings suggest that musical tapping tasks are not only capable of predicting reading and language outcomes of typical developing first-grade children, but also might even be more effective than tapping to metronome clicks. We suggest that future research on the relationship between sensorimotor synchronisation and literacy should include musical tasks that are of higher ecological validity and are more suitable for this age group.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: Menedeley Data DOI: 10.17632/5b5gd7fkwc.1.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Research Ethics Committee (REC) Faculty of Education and Psychology of ELTE. Written informed consent to participate in this study was provided by the participants' legal guardian/next of kin.

AUTHOR CONTRIBUTIONS

CK and FH conceived the presented idea. CK gathered the data and performed the statistical analyses. FH verified the analytical methods and supervised the findings of this work. All authors discussed the results and contributed to the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2021.741540/full#supplementary-material

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Dysfunctional Timing in Traumatic Brain Injury Patients: Co-occurrence of Cognitive, Motor, and Perceptual Deficits

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Timing is an essential part of human cognition and of everyday life activities, such as walking or holding a conversation. Previous studies showed that traumatic brain injury (TBI) often affects cognitive functions such as processing speed and time-sensitive abilities, causing long-term sequelae as well as daily impairments. However, the existing evidence on timing capacities in TBI is mostly limited to perception and the processing of isolated intervals. It is therefore open whether the observed deficits extend to motor timing and to continuous dynamic tasks that more closely match daily life activities. The current study set out to answer these questions by assessing audio motor timing abilities and their relationship with cognitive functioning in a group of TBI patients (n = 15) and healthy matched controls. We employed a comprehensive set of tasks aiming at testing timing abilities across perception and production and from single intervals to continuous auditory sequences. In line with previous research, we report functional impairments in TBI patients concerning cognitive processing speed and perceptual timing. Critically, these deficits extended to motor timing: The ability to adjust to tempo changes in an auditory pacing sequence was impaired in TBI patients, and this motor timing deficit covaried with measures of processing speed. These findings confirm previous evidence on perceptual and cognitive timing deficits resulting from TBI and provide first evidence for comparable deficits in motor behavior. This suggests basic co-occurring perceptual and motor timing impairments that may factor into a wide range of daily activities. Our results thus place TBI into the wider range of pathologies with well-documented timing deficits (such as Parkinson's disease) and encourage the search for novel timing-based therapeutic interventions (e.g., employing dynamic and/or musical stimuli) with high transfer potential to everyday life activities.

Keywords: traumatic brain injury, timing, attention, sensorimotor synchronization, processing speed, SDMT = Symbol Digit Modalities Test, Digit Span

INTRODUCTION

Neurocognitive timing refers to the capacity to encode, decode, and process events in time and to temporally align with the environment (Grondin, 2010; Grondin et al., 2018). Although humans are sensitive to the timing of events across multiple timescales, the ability to process time in the milliseconds-to-seconds range is particularly relevant for perception, action, and cognition (Piras et al., 2014; Bader et al., 2019). Adequate timing abilities in this range constitute a precondition for everyday activities such as walking, holding a conversation, cooking, and for virtually any kind of goal-directed behavior. Conversely, even subtle impairments in timing abilities may have a profound impact on brain function, as evidenced by perceptual, cognitive, and motor symptoms arising from timing deficits in otherwise seemingly unrelated pathologies (e.g., Attention Deficit Hyperactivity Disorder, Toplak and Tannock, 2005; Parkinson's Disease, PD, Benoit et al., 2014; Autism Spectrum Disorder, Falter and Noreika, 2011; Falter et al., 2011; Allman and Falter, 2015). This converging evidence sparked a growing interest in timing abilities as a possible cause for cognitive deficits in various neurological conditions and to develop novel therapeutic intervention strategies with a high transfer potential to numerous cognitive functions and, ultimately, daily life activities. For example, a music-based training program that employs rhythmic auditory cueing has proven effective in ameliorating both impaired motor and non-motor timing abilities in Parkinson's Disease (Nombela et al., 2013; Benoit et al., 2014; Kotz and Gunter, 2015; Dalla Bella, 2018).

Traumatic Brain Injury (TBI) refers to an acute brain injury, resulting from a blow to the head caused by external physical forces, for instance traffic collisions, falls, or violence (Carroll et al., 2004; Andriessen et al., 2010), often leading to death or lifelong disability (Maas et al., 2008; Roozenbeek et al., 2013). TBI is categorized as mild, moderate, or severe based on acute injury characteristics (e.g., loss of consciousness, post-traumatic amnesia, brain damage). Next to neurodegenerative and developmental diseases, timing can also be compromised by TBI (Pouthas and Perbal, 2004; Mioni et al., 2013a; Piras et al., 2014; Bader et al., 2019); for example, some patients report difficulties in putting events in correct chronological order (e.g., while cooking). Across all levels of severity, timing impairments and cognitive symptoms–including extreme fatigue, impaired attention, working memory, and processing speed (Wallesch et al., 2001; Hoskison et al., 2009; Witt et al., 2010; Ghajar and Ivry, 2015)–are persistent and significantly hampered in daily life (Schretlen and Shapiro, 2003; Langlois et al., 2006; Barwood and Murdoch, 2013). As these symptoms tend to co-occur, it is challenging to disentangle their relative importance and causal relation (Piras et al., 2014; Bader et al., 2019). On the one hand, timing deficits may underlie and explain the seemingly varied cognitive symptoms observed in TBI (e.g., Ghajar and Ivry, 2008); on the other, several empirical studies suggest that cognitive deficits may be the cause of more elusive timing impairments (Perbal et al., 2003; Mioni et al., 2012, 2013b, 2014). The fact that cognitive impairments may be responsible for timing deficits is based on higher variability, but not necessarily lower performance accuracy, in TBI patients than healthy controls in perceptual tasks (e.g., Anderson and Schmitter-Edgecombe, 2011; Piras et al., 2014; for a review see Mioni et al., 2014); in addition, motor timing appears to be largely unaffected (Bader et al., 2019). Taken together, this evidence seems to downsize the relevance of timing in TBI. Importantly, however, most of these studies employed timing tasks targeting stimulus durations between 4 and 60 s, often limited to the presentation of isolated time intervals (for a review see Mioni et al., 2013a). This choice likely over-emphasizes cognitive deficits as timing in this range hinges on memory and executive functions, as opposed to sub-second time intervals that are assumed to be processed more automatically (Wing and Kristofferson, 1973a). In addition, the focus on isolated intervals stands in stark contrast to the dynamic nature of most daily activities. This distinction inspires the choice of timing tasks used in other pathologies, for example PD, that typically include continuous perception (e.g., beat processing; O'Boyle et al., 1996) and continuous production tasks (e.g., paced and unpaced finger-tapping) that often require participants to adapt to changing stimulus timing. The flexibility required for these tasks depends on both automatic as well as higher-level cognitive processes; for example, compensation for relatively subtle motor timing errors may require attention and awareness in response to unexpected tempo changes, but it can also be largely automatic for more predictable sequences (Mates, 1994; Repp and Keller, 2004). Thus, not only are dynamic tasks targeting sub-second intervals closer to everyday activities, but they may also differentiate the relationship between timing and cognitive impairments.

The empirical question whether to focus on single interval or continuous timing also impacts theoretical accounts of the neural mechanisms engaged in the processing of isolated intervals as opposed to the processing of sequential intervals. Mechanisms underlying isolated interval processing are mainly discussed in the context of "internal clock models" such as the seminal scalar expectancy theory (SET; Gibbon, 1977; Church, 1984, 2003; Gibbon and Allan, 1984; Gibbon et al., 1984). These models postulate the existence of an internal pacemaker and a switch-accumulator component (Wing and Kristofferson, 1973b; Vorberg and Wing, 1996; Mioni et al., 2013a; McAuley and Fromboluti, 2014) that may rely on the functioning of fronto-striatal and thalamic connections (Meck and Benson, 2002; Buhusi and Meck, 2005). Conversely, some models of continuous timing such as dynamic attending theory (DAT; Jones and Boltz, 1989) focus on the entrainment of endogenous oscillatory activity through external rhythms, potentially without the need for a localized central clock mechanism (McAuley et al., 2006; Grondin, 2010; Honing et al., 2018). Instead, this model relies on a distributed network responsible for large scale oscillatory activity that is tightly linked to attention (e.g., Large et al., 2015; Grondin et al., 2018). Interestingly, areas and connections belonging to such integrated timing network (including prefrontal, parietal areas, and cerebellum; Inglese et al., 2005; Kinnunen et al., 2011; Schwartze and Kotz, 2013; Eierud et al., 2014; Xiong et al., 2014) are known to be commonly affected by post-traumatic diffuse axonal injury (DAI; Messé et al., 2011; Shenton et al., 2012). DAI denotes the shearing and tearing of white matter tracts that is frequently caused by TBI and has emerged as an explanation for post-traumatic symptoms persisting in the absence of clear radiological evidence of brain lesions and independent of TBI severity (Shenton et al., 2012). Because of its diffuse influence on the timing network and its independence from TBI severity, DAI may explain the variability and variety of timing symptoms in this patient population.

The current study therefore set out to investigate timing perception and production, and their relationship with cognitive measures (e.g., processing speed, attention, working memory) in a heterogenous group of TBI patients. We expected to confirm perceptual timing impairments of previous studies and then to explore patients' performance in more ecologically valid dynamic timing tasks (e.g., adaptive finger tapping). We hypothesized that these continuous tasks would lead to worse performance in TBI patients (e.g., higher tapping variability and/or lower adaptation indexes) as they rely on a large-scale timing network that is likely to be affected by DAI irrespective of TBI location and severity.

MATERIALS AND METHODS

Participants

15 patients (6F, mean age 47.53 ± 14.05 years, range: 17–64 years, group: TBI) were recruited by a neuropsychologist (SZS) at Zuyderland Medical Centre (Sittard-Geleen, Netherlands). All patients suffered from a TBI of varied severity (from mild to severe) and were, at the time of testing, in a chronic phase post-injury (mean time since injury 4.98 ± 5.23 years, range: 5 months–19 years; **Table 1**). Exclusion criteria were: (i) history of multiple traumatic brain injuries, (ii) acute phase of the pathology, (iii) perinatal brain injury (i.e., the injury occurred before, during, or shortly after birth), (iv) presence of comorbid medical or psychiatric conditions, (v) hearing difficulties not corrected by hearing aids, (vi) motor impairments preventing the use of the index finger of the dominant hand. 15 healthy controls (5F, mean age 47.53 ± 12.53, range: 23–63 years, group: HC = Healthy Controls) were recruited from a participant database at Maastricht University (UM) to individually match the patient sample as closely as possible for age, gender, and education. All controls had normal hearing and no concurrent neurological or psychiatric conditions. All participants were right handed except for one left-handed patient and one control subject. Participants were compensated for travel costs to reach the testing facilities and gave their written informed consent before participating in the study. The study was approved by the local ethical committee of Maastricht University (Maastricht, Netherlands; agreement number: Master_184_07_10_2017/A1).

Procedure

The study took place in a quiet testing room at Maastricht University to avoid distraction and contamination from external noise. The testing procedure involved: (i) an initial interview about each patient's medical condition (i.e., diagnosis, time since injury, current medication, comorbidity with medical or psychiatric conditions; see **Supplementary Material**), handedness assessment (Edinburgh Handedness Inventory; Oldfield, 1971), and music expertise; (ii) the Symbol Digit Modalities Substitution Test (SDMT; Smith, 1982) to measure impairments of attention and processing speed following TBI (Bruijel et al., 2018); (iii) the Digit Span test (Wechsler, 2008) in both forward (DS-F) and backward (DS-B) forms to obtain a reliable indication of working memory and memory span; (iv) a series of tasks from the Battery for the Assessment of Auditory Sensorimotor and Timing Abilities (BAASTA; Dalla Bella et al., 2017; Bégel et al., 2018) to investigate participants' perceptual and sensorimotor synchronization abilities. The selected tasks included:

- *Duration discrimination*: Participants listened to tone pairs (frequency = 1 kHz) to judge whether the second tone (comparison duration, range = 600–1,000 ms) lasted longer than the first (standard duration, 600 ms).
- *Anisochrony detection*: Participants judged whether sequences of 5 tones (1,047 Hz, tone duration = 150 ms, Inter-Onset Interval (IOI) = 600 ms) were isochronous (i.e., with a constant IOI) or not (i.e., the 4th tone was presented earlier than expected by up to 30% of the IOI).
- *Unpaced tapping*: To obtain a measure of preferred tapping rate and its variability, participants were asked to tap regularly at their most natural (self-chosen) rate for 60 s. This task was administered at the beginning and at the end of the BAASTA testing session to control for changes in spontaneous motor tempo due to the battery itself (e.g., induced tiredness), with the left and the right hand.
- *Paced Tapping*: Participants' ability to synchronize with a metronome (i.e., an isochronous sequence of tones) was assessed by asking them to tap with their dominant index finger to a sequence of 60 piano tones (frequency = 1,319 Hz, IOI = 600 ms).
- *Synchronization continuation*: Participants were asked to tap with their dominant index finger in synchrony with an isochronous sequence of 10 tones (IOI = 600 ms) and to keep tapping for a duration corresponding to 30 IOIs of the pacing stimulus after the pacing ceased. Each trial at a given tempo was repeated twice.
- *Adaptive tapping*: To assess the ability to adapt to a tempo change in a synchronization-continuation task, participants tapped with their dominant index finger to an isochronous sequence of 10 tones. In 40% of the trials, the tempo of the last 4 tones could either increase, decrease, or remain constant (30 or 75 ms tempo change, i.e., the sequence IOI was adjusted by adding or subtracting 30 or 75 ms); in the remaining 60% of the trials the tempo remained constant (i.e., no IOI change). Participants were asked to adapt their tapping to the tempo change, and to keep tapping at the new tempo after the end of the sequence for a time corresponding to 10 IOIs. After each trial, participants judged whether they perceived a change in stimulus tempo (acceleration, deceleration, or no change). Trials were divided into 10 experimental blocks each including 6 trials (4 with tempo change, 2 without), presented in random order.

TABLE 1 | Demographic characteristics of the patient sample and scores in the cognitive tests.

Patient	Age	Gender	Time since injury	Education	Severity	SDMT	DS-F	DS-B
0539	35	M	3 years	Middle	Severe	52	11	7
7182	61	M	6 years	High	Severe	45	16	9
0667	55	M	2 years	Low	Moderate	35	7	4
1149	47	F	6 years	Low	Severe	45	8	7
1670	17	F	4 years	Middle	Moderate	50	12	16
2515	46	F	1 years	Low	Mild	45	3	6
2848	64	M	6 months	Low	Severe	40	12	4
4383	39	F	7 years	High	Mild	45	6	5
5431	57	M	2 years	Middle	Severe	20	4	6
5719	55	M	19 years	Low	Severe	55	9	4
6303	46	F	8 years	Low	Moderate	35	7	9
7452	64	M	2 years	High	Severe	60	10	11
7860	58	F	13 years	High	Moderate to severe	50	13	12
8750	24	M	9 months	Middle	Moderate	40	8	7
9427	45	M	5 months	Middle	Mild	70	10	17

M, Male; F, female; SDMT, Symbol Digit Modality Test; DS-F, Digit-Span, forward presentation; DS-B, Digit-Span, backward presentation.

The first two tasks tested perceptual timing, while the remaining four targeted motor timing behavior. In each perceptual task, participants performed three blocks of 16 trials. Except for spontaneous tapping, all tasks were preceded by a practice trial. Please see Dalla Bella et al. (2017) for the tasks' details. All BAASTA tasks were implemented as an app on one of two identical Samsung Galaxy TAB A6 tablet devices running Android 7.0 (see also e.g., Rathcke et al., 2021). Auditory stimuli were delivered via headphones (Sennheiser HD201) at a comfortable sound level. Participants tapped directly on the surface of the tablet. The testing procedure was identical for patients and healthy controls in the above order, except for the initial interview, which was not conducted with the control group.

Data Analysis

BAASTA Perceptual Tasks

The thresholds for the duration discrimination and anisochrony detection tasks were obtained by averaging the values obtained in three blocks, expressed as percentages of the standard duration (Weber fraction). Blocks were rejected when they contained more than 30% of false alarms (i.e., participants incorrectly identified a difference in a no-difference trial).

BAASTA Production Tasks

Mean inter-tap intervals (ITIs) and their coefficient of variation (CV, obtained by dividing the ITIs SD by the mean) were calculated for each production task (see Dalla Bella et al., 2017; Bégel et al., 2018; for details on data pre-processing). For the paced tapping task, synchronization accuracy was calculated as the mean absolute asynchrony between taps and the respective pacing signal, while the corresponding standard error denoted synchronization variability. For the adaptive task, several further measures were calculated. First, the overall adaptation index (i.e., a measure of the quality of the tapping adaptation following the tempo change in the continuation phase) was calculated (Repp and Keller, 2004; Schwartze et al., 2011) for accelerations (i.e., final sequences with IOI < 600 ms—adaptation index acceleration) and decelerations (i.e., final sequences with IOI > 600 ms—adaptation index deceleration). To this end, regression lines were fitted to the slopes of the ITI functions of the final sequence tempo, and their slopes were used as adaptation indices with values of 1 indicating perfect adaptation, values lower than 1 indicating under correction, and values greater than 1 overcorrection. Second, phase correction and period correction were calculated based on Repp and Keller (2004; see also Mates, 1994); these indexes inform automatic (phase correction) vs. conscious and attentive (period correction) processes underlying adaptation to tempo changes. Third, the sensitivity index (d′) for detecting tempo changes was calculated based on the number of Hits (i.e., correct detection of a tempo change in either direction) and False alarms (i.e., incorrect detection of a tempo change). Extreme outliers in each task were defined as data points falling below the Q1 − 3*Interquartile range (IQR) or above the Q3 + 3*IQR, where Q1 is the first quartile and Q3 is the third quartile, and excluded.

Statistical Analyses

Statistical analyses were conducted in Rstudio (RStudio Team, 2020, Version 1.3.959; R Studio Inc., Boston, United States) supporting R Version 4.0.2 (R Core Team, 2020).[1] SDMT and DS scores were first corrected with the available norm scores based on education level (SDMT) and age (DS). Each dependent variable was inspected, and extreme within-group outliers (see BAASTA production task for details) were removed, while mild outlier values were retained (Bakker and Wicherts, 2014). Data were further checked for normality of the distribution by means of QQplots and Shapiro-Wilk tests (package *stats*), and for equality of variance between the groups (Levene's test; package *car*) where appropriate. As most distributions significantly

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[1] http://www.R-project.org/

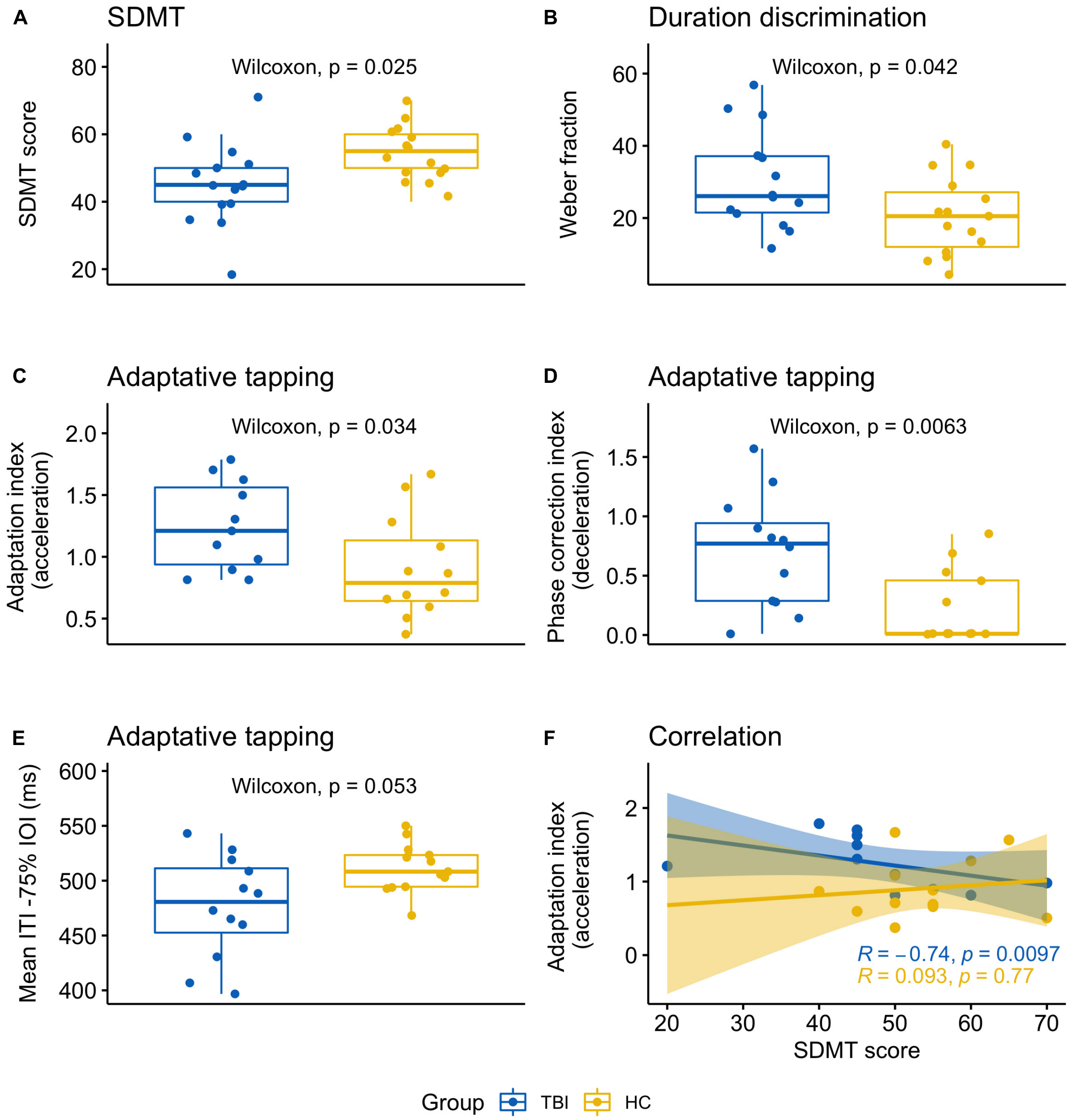

FIGURE 1 | Graphical summary of significant results indicating the main differences between TBI patients and healthy controls. **(A)** SDMT scores; **(B)** Weber fraction corresponding to the duration discrimination threshold; **(C)** adaptive tapping task, adaptation index (acceleration); **(D)** Adaptive tapping task, phase correction index (deceleration); **(E)** adaptive tapping task, mean ITI (tapping rate) for accelerating sequences (i.e., reduction of 75 ms on the standard IOI); **(F)** correlation between the adaptation index (acceleration) and the SDMT scores.

departed from normality, the Wilcoxon-Mann-Whitney test (package *stats*) was employed for group comparisons to reduce Type I errors and improve power even in the presence of mild outlier values (Bakker and Wicherts, 2014). Effect sizes are reported for significant tests as r with bootstrapped confidence intervals based on 1,000 replications (package *rcompanion;* **Supplementary Table 3**). To further corroborate the strength of significant results, we calculated and additionally reported *p*-values obtained from an n-1 jackknife resampling analysis (Tukey, 1958; package bootstrap). Spearman's rank correlation coefficients (package *stats*) were calculated among variables showing significant group differences to evaluate the relation between cognitive scores and timing performance. Bonferroni correction was applied, when necessary, to account for multiple comparisons. All results were deemed significant at an alpha level of $p < 0.05$, two-sided.

RESULTS

Cognitive Tasks

Symbol Digit Modalities Test

TBI patients performed at an average score of 45.67 ± 11.63, which is at the lower normality boundary. This result was significantly lower than for healthy controls (mean$_{HC}$ 54.00 ± 8.06; $W = 58.50$, $p = 0.025$, $r = -0.41$; **Figure 1A**) as confirmed by the jackknife estimate *p*-value (0.029 ± 0.01). Levene's test was non-significant ($p = 0.502$) despite two patients who had slightly higher (patient 9,427 = 70) or lower (patient 5431 = 20) scores compared to the rest of their group.

Digit-Span, Forward Presentation

Patients' scores were on average lower (mean_{TBI} 9.07 ± 3.47) than in healthy controls (mean_{HC} 10.53 ± 3.31), but the two groups had similar variance (Levene test $p = 0.792$), and did not differ statistically ($W = 86.5$, $p = 0.287$, $r = -0.20$).

Digit-Span, Backward Presentation

There was no significant difference between patients and controls (mean_{TBI} 8.27 ± 4.13; mean_{HC} 9.27 ± 2.49; $W = 82$, $p = 0.209$, $r = 1$, Levene test $p = 0.171$). One patient (patient 9427) obtained a moderately higher score (17); notably, patient 9427 had higher scores in the SDMT task as well.

Perceptual Timing Tasks

Duration Discrimination

Data of one patient (patient 1149) were discarded as the threshold could not be reliably estimated (see **Supplementary Table 2** for an overview of extreme or missing values in each task). The discrimination threshold was higher for TBI patients (mean_{TBI} 30.51 ± 13.72) than for healthy controls (mean_{HC} 20.51 ± 10.73). The difference between the two groups was statistically significant ($W = 152$, $p = 0.042$, $r = 0.37$; Levene's test $p = 0.485$) as further confirmed by the jackknife analysis (mean *p*-value = 0.049 ± 0.02) (**Figure 1B**).

Anisochrony Detection

The discrimination threshold could not be determined for two patients and one control (patient 4,383, patient 6,303, control,8813; **Supplementary Table 2**). In addition, one patient (1,149) had a moderately higher threshold compared to the rest of the group ($\text{mean}_{\#1149}$ 28.77 vs. mean_{TBI} 13.07 ± 7.63). Notably, for this patient there was also no valid estimation of the Duration Discrimination threshold. Yet, there was no significant difference between TBI and healthy controls (mean_{HC} 12.91 ± 7.33; $W = 90.5$, $p = 1$, $r = 0.00$; Levene's test $p = 0.953$).

Sensorimotor Timing Tasks

Unpaced Tapping

This task was performed at different testing times (beginning and end of the battery) and with different effectors (left and right hand). Thus, we performed an ANOVA with the between factor *group* and the within factors *effector* (left, right) and *time* (initial, final) for mean ITI and their CV. A summary of patients and controls who displayed extreme or missing values is reported in **Supplementary Table 2**. Mean ITIs were influenced by *effector* [$F(1, 26) = 9.64$, $p = 0.005$, $\eta^2 = 0.003$]; *post hoc* tests revealed that the interval between taps was longer when the task was done with the right hand ($\text{mean}_{\text{right}}$ 562.15, $SE = 31.16$; $\text{mean}_{\text{left}}$ 542.97 ± 31.16; $t = -3.10$, $p = 0.005$). In addition, the interaction between time and effector reached significance [$F(1, 26) = 4.75$, $p = 0.039$, $\eta^2 = 0.001$]: a simple effects analysis revealed no difference between left and right hand during the initial task ($p = 0.84$) but a significant difference in the final task ($t = -3.76$, $p = 0.002$, Tukey corrected; left hand t2 = 509.96, $SE = 34.28$; right hand t2 = 541.42, $SE = 34.28$). No other effects were significant (all ps > 0.07). Variability (CV_{iti}) was not significantly influenced by any of the factors (all $p > 0.07$). However, variance between the TBI group and healthy controls was significant [Levene's test: $F(1, 27) = 5.21$, $p = 0.03$], showing a generally higher variability in TBI patients.

Paced Tapping

Mean ITIs were very similar for TBI (mean_{TBI} 600.26 ± 1.55) and controls (mean_{HC} 599.80 ± 0.54; $W = 85$, $p = 0.255$, $r = 0.21$). Levene's test was close to significance ($p = 0.051$), indicating slightly higher variance in the patients' group. Motor variability was not significantly different between patients and controls (mean_{TBI}.15 ± 0.17; mean_{HC}.05 ± 0.01; $W = 143$, $p = 0.102$, $r = 0.30$), yet Levene's test was ($p = 0.035$), indicating greater variance in patients. Synchronization accuracy (i.e., mean absolute asynchronies) was, on average, higher in the TBI group (mean_{TBI} 10.74 ± 7.18) than in the control group (mean_{HC} 8.67 ± 4.91), but this numerical difference was also not significant ($W = 126$, $p = 0.590$, $r = 0.10$). Lastly, synchronization variability (i.e., SE of asynchrony between tap and pacing signal), albeit higher in TBI (mean_{TBI} 1.14 ± 0.94) than in controls (mean_{HC} .77 ± 0.21), was not significantly different ($W = 110$, $p = 0.369$, $r = 0.17$).

Adaptive Tapping

The adaptation index (acceleration) was significantly different between patients and controls (mean_{TBI} 1.25 ± 0.36, mean_{HC} 0.91 ± 0.41; $W = 101$, $p = 0.034$, $r = 0.39$; average jackknife $p = 0.04 ± 0.01$; **Figure 1C**). In addition, the phase correction index for tempo decelerations was significantly lower for TBI compared to controls (mean_{TBI} .70 ± 0.47, mean_{HC} .22 ± 0.31; $W = 127.50$, $p = 0.006$, $r = 0.50$; **Figure 1D**). The jackknife estimate confirmed the robustness of this result (average jackknife $p = 0.008 ± 0.001$). The mean ITI in the slowest tempo condition (−75% IOI) was close to significance ($W = 42$, $p = 0.053$, $r = -0.36$; **Figure 1E**), with TBI patients tapping faster compared to controls (mean_{TBI} 476.03 ± 46.82; mean_{HC} 511.47 ± 22.24). Levene's test was significant ($p = 0.023$), indicating different variance between the groups. Tapping variability (CV ITI) and judgment accuracy (d-prime) were not significant.

No other significant differences were observed in this task (all *p*s > 0.183).

Synchronization Continuation

There were no significant differences between patients and controls in any of the outcome variables for this task (all *p*s > 0.221).

Correlations

We conducted a correlation analysis between SDMT and the timing tasks which significantly differed between groups. These included one perceptual task (duration discrimination) and two variables from the adaptive task (adaptation index acceleration, phase correction index deceleration) for a total of three repeated tests. When considering data from both groups, SDMT was not significantly correlated with any other measure; however, in the TBI group—but not in the healthy controls—a significant negative correlation emerged between SDMT and the adaptation index for accelerating sequences ($rs = -0.74$, $p = 0.010$; Bonferroni correction for multiple comparisons: $0.05/3 = 0.017$; **Figure 1F**).

DISCUSSION

The current study set out to investigate timing abilities in TBI patients. We tested 15 patients in a series of timing perception and production tasks and compared their performance with that of age-, gender-, and education-matched healthy controls. Our results confirm functional impairments in the TBI group, affecting both cognitive as well as perceptual and motor timing abilities. Cognitively, patients showed deficits in processing speed, as indicated by lower scores in the SDMT compared to controls. In the timing domain, TBI patients displayed higher discrimination thresholds for sounds differing in duration. Patients also showed a reduced ability to adjust their finger tapping in response to tempo changes in auditory pacing sequences. This motor timing deficit further correlated with the SDMT score. Not only do our results confirm a clear impairment in processing speed and perceptual timing following TBI, but they also identify deficits in motor timing, which suggests a more generalized timing deficit than previously hypothesized in this pathology.

The results thus confirm previous evidence showing perceptual timing deficits in TBI (e.g., Mioni et al., 2013b) and higher performance variability in the patient group (Anderson and Schmitter-Edgecombe, 2011; Mioni et al., 2014; Piras et al., 2014). Overall increased variability in patients, in terms of a greater variance between groups, was evidenced by significant Levene's tests in several tasks, namely unpaced, paced, and adaptive tapping. Notably, all these tasks tested motor timing, while group variance did not differ in either cognitive or perceptual timing tasks. These results therefore provide first important evidence of possible motor timing impairments. This is further supported by the finding that patients could not compensate for tempo changes in adaptive tapping. In this task, the adaptation index for accelerating sequences indicated a difficulty in "keeping up" with the pacing sequence. For decelerating sequences (i.e., sequences in which tempo was slowing down), patients had difficulties in applying phase correction to adapt to the changes. Yet, we must caution that the overall heterogeneity of the patient sample may be reflected in these results. Future studies need to further explore these aspects in larger and more homogeneous participant groups. Still, these results are particularly important for at least two reasons: first, motor timing has been typically considered as spared in TBI (Bader et al., 2019). For example, Perbal et al. (2003) found no motor deficit–but higher variability–in production or reproduction tasks in severe TBI (see also Pouthas and Perbal, 2004); similarly, Bader et al. (2019) found no evidence of motor timing deficits in mild TBI patients in a paced tapping task. Second, phase correction is considered a largely automatic process that is independent of cognitive functioning (Repp and Keller, 2004). By identifying this potentially "purer" timing deficit, the latter evidence speaks against the hypothesis that timing impairments may be the sole result of a failure in memory, attention, or other cognitive functions (Perbal et al., 2003; Mioni et al., 2012, 2013b, 2014).

It is possible that the adaptive task employed in the current experiment (Schwartze et al., 2011), may be more sensitive to subtle impairments as it targets the dynamic ability to flexibly recognize and adapt to tempo changes in continuous stimulation. As such, it may be better suited to more closely probe the timing requirements of daily life activities affected by TBI (e.g., wrapping a present; Schwartz et al., 1998). Alternatively, it is possible that previous studies failed to identify motor timing deficits as they exclusively targeted mild TBI (Bader et al., 2019; but see Perbal et al., 2003, for an example of severe patients). However, this explanation would stand in contrast with the hypothesis that an underlying DAI may affect the timing network, since DAI is assumed to be independent from TBI severity (Ghajar and Ivry, 2008; Shenton et al., 2012). Unfortunately, DAI can only be assessed by means of dedicated neuroimaging techniques such as Diffusion Tensor Imaging (DTI; Shenton et al., 2012). Future studies should therefore take advantage of DTI to evaluate the relationship between the extent of DAI and possible timing and cognitive deficits. The extreme variety observed in a typical TBI population, both in terms of symptoms and type of underlying lesion, calls for a highly individualized approach to identify possible patterns of co-occurring DAI and timing or cognitive deficits.

In the current study we observed deficits in processing speed, in line with previous accounts (e.g., Wallesch et al., 2001; Hoskison et al., 2009; Witt et al., 2010; Ghajar and Ivry, 2015). Most importantly, we report a correlation between SDMT scores and the adaptation index, reflecting lower adaptation abilities in patients with higher processing speed scores. This result stands in contrast with previous accounts showing that timing deficits go hand in hand with cognitive dysfunctions (e.g., Mioni et al., 2013b). While we clearly cannot use the current result to establish causality or independence between these measures, we suggest that timing and cognitive deficits in TBI may constitute a more complex relationship than previously hypothesized. Further, we suggest that dynamic timing tasks, closer matched to everyday life activities, may provide further insights into the complex symptomatology of this pathology.

Lastly, we put forward some limitations of the current study. First, our sample size was relatively small, due to the difficulty in patient recruitment. While our results are largely in line with the previous literature, a larger sample might help to strengthen some of our conclusions, particularly for those tasks (e.g., adaptive tapping) that are novel in the TBI literature. Hence, we highly encourage future studies to replicate our results within a larger group of participants. Second, we could not directly test specific hypotheses based on the neurological damage caused by TBI and/or DAI; as previously said, future studies should consider introducing neuroimaging (e.g., DTI) to further characterize the relationship between neurological (e.g., location and extent of the lesion, white matter integrity, etc.), cognitive, and timing deficits in TBI. A better characterization of individual deficits may allow informing individualized intervention strategies that consider each patient's residual abilities as well as recovery potential. Third, our patient sample was quite heterogeneous. While we selected the patients in the current study to test for specific timing impairments irrespective of TBI severity levels, it is possible that heterogeneity contributed to the observed increased variability in most tasks in the patient group. Future studies should address this possibility by targeting several patient groups, a larger sample size, and more homogeneous level of TBI severity.

CONCLUSION

In conclusion, the current study found evidence of cognitive, perceptual, and motor timing deficits in TBI patients. As a next step, we suggest that future studies should systematically explore the complex relationship between TBI symptoms and their underlying neurological causes. In doing so, it would be important to consider possible therapeutic approaches; in particular, we propose that timing, due to its fundamental role in everyday life, might represent an overarching principle with great potential for therapeutic impact, mirroring its application in other pathologies such as PD (Benoit et al., 2014; Dalla Bella, 2018).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by the Ethical committee of Maastricht University, faculty of Psychology and Neuroscience (Maastricht, The Netherlands; agreement number: Master_184_07_10_2017/A1). The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

MS and SK developed the theoretical framework. LV analyzed the data and wrote the manuscript. SS and IW recruited the participants and coordinated data collection. All authors conceived and developed the experiment and provided critical feedback on the research, analysis and manuscript.

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SUPPLEMENTARY MATERIAL

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Modeling Frequency Reduction in Human Groups Performing a Joint Oscillatory Task

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In human groups performing oscillatory tasks, it has been observed that the frequency of participants' oscillations reduces when compared to that acquired in solo. This experimental observation is not captured by the standard Kuramoto oscillators, often employed to model human synchronization. In this work, we aim at capturing this observed phenomenon by proposing three alternative modifications of the standard Kuramoto model that are based on three different biologically-relevant hypotheses underlying group synchronization. The three models are tuned, validated and compared against experiments on a group synchronization task, which is a multi-agent extension of the so-called mirror game.

Keywords: joint action, human behavior, modeling, Kuramoto oscillators, slowing down

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1. INTRODUCTION

Joint action can be regarded as any form of embodied social interaction where two or more individuals tend to coordinate their movements, often in a highly synchronized way in space and time, in order to reach a common goal. This phenomenon is observed in several everyday scenarios, including music ensembles (Loehr et al., 2011) and team rowing (Cuijpers et al., 2019), and has potential implications in group rehabilitation (Virta et al., 2008; Calabrese et al., 2021).

Physics and social science offer several mathematical frameworks to describe collective oscillatory perceptuo-motor behaviors in joint action (Néda et al., 2000; Sumpter, 2006; Castellano et al., 2009; Ashwin et al., 2016). Namely, both the Haken-Kelso-Bunz (HKB) and the heterogeneous Kuramoto oscillators have been successfully employed to explain how synchronization emerges in human groups performing oscillatory tasks (Kuramoto, 1984; Haken et al., 1985). For instance, Alderisio et al. (2017a) found that the Kuramoto model was able to capture the type and level of group coordination that was experimentally observed, depending on group homogeneity and the visual coupling among group members. Although effective in reproducing the level of synchronization in the group, this model predicts synchronization of the group oscillatory motion to the average value of the individual characteristic frequencies when playing solo. This is in contrast with the joint-action literature that shows how cooperative actions require a more selective and slower mechanism compared to individual movements (Cavallo et al., 2014).

Slowing down of individuals' motion when coordinating with others has been widely observed across several tasks, including applause (Néda et al., 2000), where it has been observed that synchronization is achieved through a period doubling of the clapping rhythm, or in finger tapping, where participants were found to tap faster alone than when involved in rhythmic cooperative tasks (Coey et al., 2016), as well as in human-robot interactions (Lorenz et al., 2011). In addition, a recent experimental study on intentional group synchronization showed that humans reduce the frequency of oscillation of their fingers when they are asked to attain unison in space and time (Bardy et al., 2020), thereby suggesting that individuals modulated their behavior to maximize perceptual coupling and increase their level of synchronization.

Motivated by these experimental findings, we propose three new versions of the standard Kuramoto model, each of them anchored into a specific and functionally relevant hypothesis. The goal is to obtain a model that is able to capture at the same time (i) the level of coordination observed in human groups performing oscillatory tasks, and (ii) the reduction in the frequency of oscillation when compared to a solo performance. After developing three alternative models built around different biologically-relevant explanations of the slowing down phenomenon, we test them against experiments on a group synchronization task, a multi-agent extension of the so-called mirror game (Noy et al., 2011). Specifically, using the three collected datasets, we experimentally tuned, validated, and compared the three models, in terms of their ability to match the synchronization levels and oscillation frequency reduction observed in the experiments.

2. SYNCHRONIZATION METRICS

In what follows, we quantify the level of coordination in a group of N players, whose phases at time t are denoted as $\theta_1(t), \dots, \theta_N(t)$. The *order parameter* $0 \leq r(t) \leq 1$ describing the phase cohesiveness of the group at time t is defined as follows:

$$r(t) = \left| q(t) \right|, \tag{1}$$

where

$$q(t) = \frac{1}{N} \sum_{i=1}^{N} e^{j\theta_i(t)}, \tag{2}$$

whereas the phase

$$\psi(t) = \tan^{-1} \frac{\mathrm{Im}\{q(t)\}}{\mathrm{Re}\{q(t)\}} \tag{3}$$

associated to the order parameter will be the *group phase* at time t. The order parameter quantifies the level of phase synchronization in the group, with $r(t) = 1$ corresponding to the players sharing the same phase at time t.

The *level of frequency coordination* of the entire ensemble at time t can be quantified as

$$\rho(t) := \frac{1}{N} \left| \sum_{i=1}^{N} e^{j\Delta\phi_i(t)} \right|, \tag{4}$$

where $\Delta\phi_i(t) := \phi_i(t) - \bar{\phi}_i(t)$, with

$$\bar{\phi}_i(t) := \tan^{-1} \frac{\mathrm{Im}\{\bar{\phi}_i'\}}{\mathrm{Re}\{\bar{\phi}_i'\}}. \tag{5}$$

Differently from Richardson et al. (2012), $\bar{\phi}_i'$ is the moving average over a time window w of the relative phase $\phi_i(t) := \theta_i(t) - \psi(t)$ of oscillator i with respect to the group, that is,

$$\bar{\phi}_i'(t) := \frac{1}{w} \sum_{l=t-w}^{t} e^{j\phi_i(l)}, \tag{6}$$

The index $0 \leq \rho(t) \leq 1$ gives information on the variability of the phase mismatch among all oscillators. Namely, $\rho(t)$ equal to 1 corresponds to a perfect matching of the oscillation frequencies at time t.

3. MODELING HUMAN GROUP SYNCHRONIZATION

The emergence of synchronization in interacting groups of humans performing oscillatory tasks has been successfully captured by networks of nonlinearly coupled heterogeneous Kuramoto oscillators (Kuramoto, 1984; Alderisio et al., 2017a):

$$\dot{\theta}_i(t) = \omega_i + c \sum_{j=1}^{N} \sin(\theta_j(t) - \theta_i(t)), \tag{7}$$

where θ_i is the phase associated to the motion of player i, ω_i represents its natural frequency, and c the coupling gain describing the intensity of the interaction between the agents. However, this standard model predicts frequency synchronization onto the average value of the individual characteristic frequencies (Bullo, 2018), at a distance from the experimental observation of a frequency reduction in group oscillations (Lorenz et al., 2011; Cavallo et al., 2014; Coey et al., 2016; Bardy et al., 2020), thus suggesting that model (Equation 7) needs to be appropriately modified.

Toward capturing this frequency reduction, we propose three different extensions of the standard Kuramoto model, each acting on one of the three salient components of a complex system, that is, the *individual dynamics*, the *interaction topology*, and the *communication protocol*. Each of the extensions, which we will call Model 1, 2, and 3, respectively, is based on one of three main biologically-relevant explanations of the observed frequency reduction (Foulkes and Miall, 2000; Chafe et al., 2010; Serences and Kastner, 2014). In particular, the first two models will relate this phenomenon to behavioral plasticity, that is, the ability each individual has of adjusting to complex environmental conditions, whereas the latter to the inherent perception-action delays.

3.1. Model 1: Behavioral Plasticity as the Result of Individual Adaptability

Behavioral plasticity is crucial to achieve successful coordination in humans, and it has been posited that such human ability is the result of movement adaptation (Van Der Steen and Keller, 2013), whereby our motor system needs to deal with muscular fatigue, external loads, or changes in our sensory systems guiding the movement (Foulkes and Miall, 2000). This adaptation is often associated with a slower individual motion, which favors synchronization and fosters a successful interaction with others (Van Braeckel et al., 2007). From a social perspective, interpersonal entrainment leads to de-individuation and to the formation of a common group identity amongst partners, motivating the individuals to adapt their behavior (Cross et al., 2019).

Here, we model the observed frequency reduction as the result of an adaptive mechanism where individuals in the group reduce their natural frequencies until a desired degree of phase synchronization is achieved. This is quantified by a threshold value $\widetilde{r} > 0$ of the order parameter (Equation 1), so that model (Equation 7) becomes

$$\begin{aligned} \dot{\theta}_i(t) &= \omega_i(t) + c \sum_{j=1}^{N} \sin(\theta_j(t) - \theta_i(t)), \\ \dot{\omega}_i(t) &= \begin{cases} -\frac{1}{r^2(t)}\omega_i(t), & \text{if } r(t) < \widetilde{r}, \\ 0, & \text{otherwise.} \end{cases} \end{aligned} \tag{8}$$

Note that the farther the group is from the desired level of coordination $\widetilde{r}$, the larger the decrease in individual frequencies will be.

3.2. Model 2: Behavioral Plasticity as a Result of Selective Attention

An alternative explanation of human behavioral plasticity lies in *selective attention*, which is the ability to focus on one source of information while disregarding the others (Portas et al., 1998). This neural mechanism allows to complete group tasks successfully (Capozzi et al., 2016), coping with i) the noise affecting the sensory neurons that encode external stimuli, and ii) the fact that only the most relevant visual stimuli can be processed and translated into actions by the motor system (Serences and Kastner, 2014).

Both factors reduce the speed and accuracy of perception-action responses, and thus we propose to weigh the interactions among the individuals to prioritize the relevant stimuli:

$$\dot{\theta}_i(t) = \omega_i + c \sum_{j=1}^{N} w_{ij} \sin(\theta_j(t) - \theta_i(t)). \tag{9}$$

In this expression, $w_{ij} \geq 0$ quantifies the attention level that agent i devotes to the motion of agent j. Here, we ground the selection of these weights in the theory of *motor variability* (Bernstein, 1966), which is viewed as the result of adaptive and compensatory mechanisms to e.g., cope with perturbations, reduce injury risks, or improve coordination (Bardy and Laurent, 1998; Bartlett et al., 2007). In oscillatory tasks, motor variability in each individual, say i, can be simply quantified in terms of the standard deviation σ_i of the oscillatory frequency (Longo and Meulenbroek, 2018), which we computed from experiments performed by a single individual (from now on denoted as the *solo* experimental condition). We then hypothesize that agents with a larger standard deviation will be more prone to adjust their rhythm to that of their neighbors. At the same time, recent findings indicated that individuals involved in a joint action adjust the variability of their own movements depending on the predictability of their partners' movements (Sabu et al., 2020), thus suggesting that the attention that agent i devotes to agent j is inversely proportional to the standard deviation σ_j. Accordingly, we propose to select w_{ij} in Equation (9) as

$$w_{ij} = \frac{\sigma_i}{\sigma_j}. \tag{10}$$

Indeed, our hypothesis here is that the standard deviation in solo is the proxy of the individual motor signature (Slowinski et al., 2016) of each individual, thereby the ratio between these standard deviation is what the individual actually perceives when interacting with the others.

3.3. Model 3: Perception-Action Delays

Previous work has considered the presence of delays in the neuro-communication pathways for modeling oscillatory behavior (Izhikevich, 2007; Timms and English, 2014; Petkoski and Jirsa, 2019; Slowinski et al., 2020). In fact, multilevel crosstalk represents an important neural basis for motor control (Banerjee and Jirsa, 2007), since multi-sensory processing is not instantaneous and involves participation of different senses (e.g., vision, hearing) to facilitate the perception of environmental stimuli (Thakur et al., 2016).

As a third alternative, we propose to explain the reduced frequency observed in groups of individuals synchronizing their movements by introducing a perception-action delay in the standard Kuramoto model (Equation 7) as follows:

$$\dot{\theta}_i(t) = \omega_i + c \sum_{j=1}^{N} \sin(\theta_j(t-\tau) - \theta_i(t)), \tag{11}$$

where the neuro-motor delays are captured by the parameter τ, which corresponds to the time required by an agent i to track the position of an agent $j \neq i$, process this information, and modulate its own action accordingly. Estimating the delay associated with perception-action has been the subject of extensive literature in neuroscience (Clarke et al., 1999), psychology (Brown et al., 1999), and behavioral science (Marzi et al., 1991; Li et al., 2012), with all studies agreeing that τ should lie in the range $[5, 300] \times 10^{-3}$ s. Note that the delay might be also modeled through a phase shift in the coupling function (Izhikevich, 2007), but we preferred to explicitly model it to clarify that it is a perception delay, whereby in Equation (11) the delay parameter τ affects θ_j (the phase of individual j perceived with delay τ by individual i) and not θ_i (the own phase of individual i).

4. METHODS

4.1. Data Collection

We considered a dataset coming from experiments on group motor coordination performed at the University of Naples Federico II. The experiments were run via the computer-based architecture *Chronos* (Alderisio et al., 2017b), which allows remote motor coordination between players in the absence of social (visual and/or acoustic) interaction. The Chronos

FIGURE 1 | Experimental setup- Chronos. Participants had to oscillate and synchronize the index finger of their preferred hand over a Leap Motion controller while being virtually connected with the others through the platform Chronos.

TABLE 1 | Mean individual frequencies $\bar{\omega}_i$ in the solo condition.

Player	$\bar{\omega}_i$ **(rad/s)**
1	3.40 ± 1.55
2	3.04 ± 0.11
3	6.36 ± 0.58
4	3.34 ± 0.21
5	9.91 ± 0.68
Average	5.21 ± 2.96

TABLE 2 | Group synchronization frequency $\bar{\omega}_g$, order parameter $\bar{r}$ and frequency synchronization index $\bar{\rho}_g$ observed in the experiments.

$\bar{\omega}_g$ **(rad/s)**	$\bar{r}$	$\bar{\rho}$
2.97 ± 0.08	0.90 ± 0.08	0.97 ± 0.01

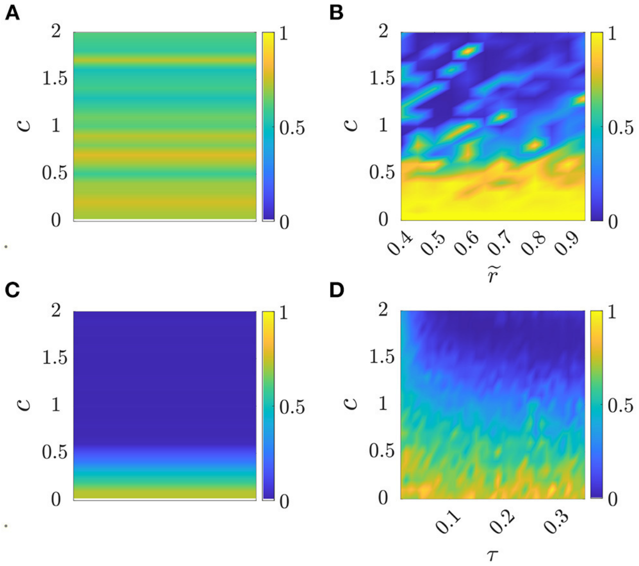

FIGURE 2 | Cost function J_m as a function of parameter selection, see Section 4.2.1. Panel **(A)** corresponds to Standard Kuramoto ($\Pi_s = \{c\}$), **(B)** to Model 1 ($\Pi_1 = \{c, \tilde{r}\}$), **(C)** to Model 2 ($\Pi_2 = \{c\}$), and **(D)** to Model 3 ($\Pi_3 = \{c, \tau\}$). The values of the cost function J_m are averaged over 10 simulated trials in each parameter set $\mathcal{A}_m$, see **Table 3** for the optimal parameter values for each model.

TABLE 3 | Optimal parameter values for each model.

Standard Kuramoto	**Model 1**		**Model 2**	**Model 3**	
c^*	c^*	$\tilde{r}^*$	c^*	c^*	τ^*
1.6	1.3	0.55	1.1	1.9	0.17

platform is a computer-based architecture consisting of different software/hardware devices. A central server unit receives position data from the clients (i.e., players), captured by a low-cost position sensor- Leap Motion device (Guna et al., 2014). The positions of each agent are then broadcast to the others, through a Wi-Fi network, and appear on the monitor of each individual personal computer (see **Figure 1**).

Task description. The dataset referred to experiments with groups of 5 participants that were asked to move their index finger on a Leap Motion controller so as to move a ball on the screen representing their own avatar, oscillating from left to right and vice versa. Each experiment started with a 30 s solo session to capture the natural frequency of each individual, identified as its average frequency across 7 solo trials, see **Table 1**. The second session of the experiments (6 trials, 30 s each) was devoted to investigating group synchronization. Participants were connected through the software platform Chronos and were asked to oscillate their fingers in synchrony with the others. Namely, they were instructed to "Synchronize the movement of your finger from left to right with the movement of the others, as naturally as possible, as if you could do it for 30 min" (see **Figure 1**). A demonstration was performed to make sure the task was understood by each participant. Moreover, volunteers were separated by barriers and wore headphones playing white noise. Albeit the Chronos platform can be used to manipulate the on-screen information for each player to implement different interaction topologies, here we focused on a complete topology where all players have access to the current position of all the other group members. The experiment was carried out according to the principles expressed in the Declaration of Helsinki. All participants provided their written informed consent to participate in the study.

Preprocessing the data. The position time-series of the players was sampled at 10 Hz, interpolated with a spline to obtain a 100 Hz dataset, and then processed by a Butterworth filter with a cutoff frequency that is twice the typical one associated to human natural movement ($\sim$ 3 Hz). The Hilbert transform (Kralemann et al., 2008) was used to reconstruct the phase associated to each agent from its position time series.

4.2. Parameterizing the Models

Comparing **Tables 1**, **2**, we observe that participants reduce the frequency of their oscillations when coordinating with their partners. Independent t-tests run between solo and group frequencies in each group showed significant differences [$t_{(11)} = 17.07$, $p < 0.001$]. We observed that the reduction in group frequency was beneficial for coordination, since participants reach a synchronization level significantly different from that obtained when the phases are randomly extracted from a uniform distribution in $[0, 2\pi]$, that is, $r = 0.40 \pm 0.20$.

The standard Kuramoto model (Equation 7) is capable of reproducing the emergence of coordination when agents interact but it fails to capture the observed slowing down in their motions' frequencies. In what follows, we calibrate Models 1–3 and the standard Kuramoto model (Equation 7) on the collected dataset. Then, we perform an ANOVA to assess whether the new models yield a significant improvement over the standard one, and to evaluate which of them is more effective in reproducing the observed reduction in the oscillation frequency among the players when in group.

4.2.1. Tuning the Model Parameters

We follow a different procedure for the standard Kuramoto model and for Models 1–3. As in the standard model the frequencies will always converge to the mean (Bullo, 2018), we select the optimal coupling gain $c^\star$ of model (Equation 7) so that the model best captures the observed phase and frequency synchronization level in a mean square sense. Namely, to find the optimal $c^\star$, we performed 10 simulations for each candidate value c, varied in $[0, 2]$ with step 0.1 with the same duration and sampling as in the experiment. In each simulation, the initial phases were randomly picked from a uniform distribution in $[0, 2\pi]$, whereas the natural frequency ω_i of player i from a Gaussian distribution with mean and standard deviation corresponding to their sample estimates computed in the solo condition. For the set of simulations, we computed $\bar{r}^{\,\text{sim}}$ and $\bar{\rho}^{\,\text{sim}}$ representing the averages across time and simulated trials of the synchronization metrics r and ρ_g defined in Equations (1) and (4), respectively. Namely, we computed

$$c_s^\star = \arg\min_c J_s(c), \tag{12}$$

where

$$J_s(c) = \lambda\left(\frac{\bar{r}^{\,\text{exp}} - \bar{r}^{\,\text{sim}}(c)}{\bar{r}^{\,\text{exp}}}\right)^2 + (1-\lambda)\left(\frac{\bar{\rho}^{\,\text{exp}} - \bar{\rho}^{\,\text{sim}}(c)}{\bar{\rho}^{\,\text{exp}}}\right)^2 \tag{13}$$

where $\bar{r}^{\,\text{exp}}$ and $\bar{\rho}^{\,\text{exp}}$ are the averages across time and trials of the indexes r and ρ. This cost function measures the agreement in phase and frequency synchronization between simulations and experiments. Parameter λ is set to 0.30 to bias parameter choice toward a better agreement on the average ρ, that is, on the level of frequency synchronization.

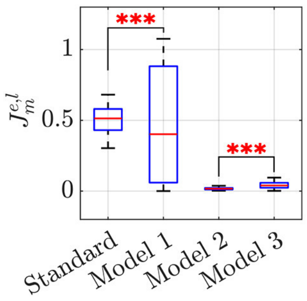

FIGURE 3 | Boxplots of $J_m^{e,l}$. Each sample represents the value of the cost function $J_m^{e,l}$ for all the possible pairs of experimental and simulated trials, to compare the effectiveness of the l-th simulated trial in reproducing the e-th experimental data in each model m. A triple star corresponds to $p < 0.001$. See **Table 4** for the average $J_m^{e,l}$ and its standard deviation, in each model m.

Models 1–3 have been introduced to also capture the reduced oscillation frequency when in group, therefore a different cost function is needed for tuning their parameters. Let us denote with Π_m, $m \in \{1, 2, 3\}$, the set of tunable parameters of model m. Namely, we have $\Pi_1 = \{c, \widetilde{r}\}$, $\Pi_2 = \{c\}$, and $\Pi_3 = \{c, \tau\}$. Further, we denote as $\mathcal{A}_m$ the set of admissible values for the parameters of model m. Specifically,

- the coupling gain c is varied in the range $[0, 2]$ with step 0.1, consistent with the choice made for the standard Kuramoto model;
- the threshold $\widetilde{r}$ in Equation (8) is varied in $[0.40, 0.95]$ with step 0.05, where 0.40 is the expected order parameter when the phases of 5 oscillators are randomly extracted in $[0, 2\pi]$, and 0.95 corresponds to all phases within an angle of $\pi/3$ rad;
- the information delay τ is varied in the interval $[0.01, 0.35]$ with step 0.01. The extrema of the interval have been selected on the basis of the transmission delays typically reported in the literature on the sensorimotor system.

As in the case of the standard Kuramoto model, we performed ten simulations for each proposed model and combination of parameters. The selection of the initial phases and natural frequencies was performed as above and, for each model, we then computed $\bar{r}^{\,\text{sim}}$ and $\bar{\rho}^{\,\text{sim}}$. In addition, we computed the oscillation frequency $\overline{\omega}_g^{\,\text{sim}}$ in the group averaged over time and simulated trials. Then, to calibrate the parameters of model $m \in \{1, 2, 3\}$, we considered the following cost function:

$$J_m(\Pi_m) = J_s(\Pi_m) + \left(\frac{\overline{\omega}^{\,\text{exp}} - \overline{\omega}^{\,\text{sim}}(\Pi_m)}{\overline{\omega}^{\,\text{exp}}}\right)^2, \tag{14}$$

TABLE 4 | Results of the ANOVA comparing the cost functions $J_m^{e,l}$ for each of the models.

Anova results	Standard kuramoto	Model 1	Model 2	Model 3
$F_{(3,134)} = 60.64$, $p < 0.001$	0.51 ± 0.11	0.46 ± 0.37	0.02 ± 0.01	0.04 ± 0.02

We report the F-statistics, p-value, and the mean and standard deviation of $J_m^{e,l}$.

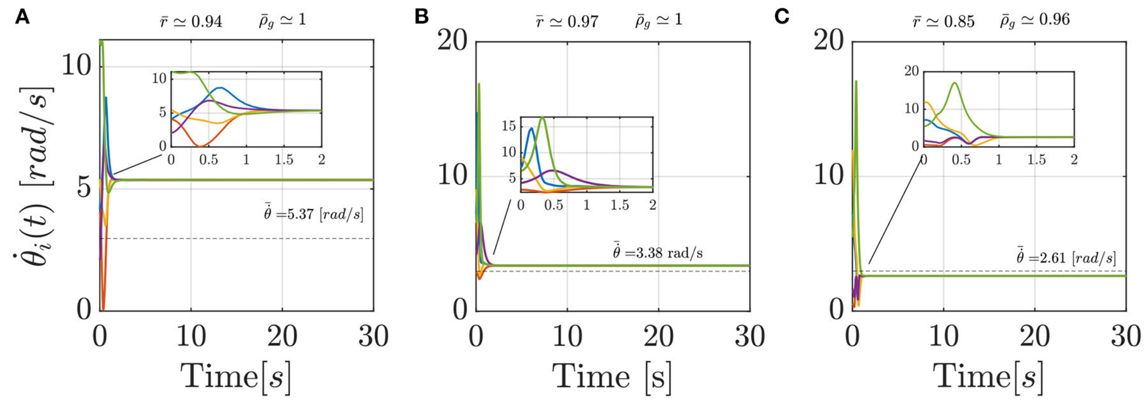

FIGURE 4 | Comparison between three sample simulated trials of the Standard Kuramoto **(A)**, Model 2 **(B)**, and Model 3 **(C)**, respectively. In each panel, the dashed line reports the average experimental group frequency $\overline{\omega}_g^{\text{exp}}$ whereas on the top the order parameter r and the group frequency index ρ_g, in their averaged values, are detailed.

where $\overline{\omega}_g^{\text{exp}}$ is the oscillation frequency in the group averaged over time and experimental trials. Compared with the cost function J_s used to calibrate the standard Kuramoto model, this cost function is complemented by a second term that accounts for the model ability to capture the average group frequency observed in the experiment. The color maps in **Figure 2** show for each parameter combination and model the value of J_m.

For all models $m \in \{1, 2, 3\}$, we selected the parameter combination $\Pi_m^\star$ yielding the lowest value of J_m, that is,

$$\Pi_m^\star = \arg\min_{\Pi_m \in \mathcal{A}_m} J_m(\Pi_m). \tag{15}$$

In **Table 3**, we report the optimal parameter values corresponding to the minimum cost function for each model and dataset.

5. RESULTS

Here, we compare how each of the models captures the experimental data by evaluating the cost function (Equation 14) for each pair (e, l) of experimental and simulated trials. Specifically, denoting N_t the number of trials of the dataset, we compute

$$J_m^{e,l} = \left(\frac{\omega_e^{\text{exp}} - \omega_{ml}^{\text{sim}}(\Pi_m^\star)}{\omega_e^{\text{exp}}}\right)^2 + (1-\lambda)\left(\frac{\rho_e^{\text{exp}} - \rho_{ml}^{\text{sim}}(\Pi_m^\star)}{\rho_e^{\text{exp}}}\right)^2 + \lambda\left(\frac{r_e^{\text{exp}} - r_{ml}^{\text{sim}}(\Pi_m^\star)}{r_e^{\text{exp}}}\right)^2 \tag{16}$$

for all $m \in \{s, 1, 2, 3\}$, $e, l \in \{1, \ldots, N_t\}$, where $\Pi_m^\star$ are the optimal parameters reported in **Table 3**, ω_e^{exp}, ρ_e^{exp} and r_e^{exp} represent group frequency, level of frequency coordination, and order parameter recorded in the e-th experimental trial, respectively, whereas ω_{ml}^{sim}, ρ_{ml}^{sim} and r_{ml}^{sim} are the corresponding values in the l-th simulated trial. For each model m, we evaluated the cost function (Equation 16) for all the 36 possible pairs of experimental and simulated trials, and then ran an ANOVA test on the distribution of $J_m^{e,l}$ to compare the effectiveness of each model in reproducing the experimental data. The outcome of the analysis is reported in the boxplot in **Figure 3** and **Table 4**, which show a significant difference among the model performances ($p < 0.001$).

A closer look at the results indicate that Models 2 and 3 should be preferred over the standard Kuramoto, since pairwise comparisons show that they have statistically different performances (*post-hoc* Bonferroni tests, $p < 0.001$), with a notable reduction in the average value of the cost function (Equation 16), see **Table 4**. Model 1, instead does not prove better than the standard Kuramoto, whereby we cannot reject the null hypothesis of equivalent performances ($p = 0.50$). In terms of average values, Model 2 outperforms also Model 3, albeit their performances are not statistically different. To illustrate how Models 2 and 3 are capable of better matching the average experimental value compared with the standard Kuramoto model, we report in **Figure 4** their dynamics in a sample simulated trial.

6. DISCUSSION

In this article, starting from the observation that human agents performing a joint oscillatory task together slow down their motion, we proposed three different models to capture this phenomenon based on different biologically-relevant hypotheses underlying sensorimotor group synchronization. The results presented in this manuscript suggest that two models emerge as the ones that better capture the experimental observations, that is, Model 2, which includes a mechanism of selective attention toward the players that are more consistent in their solo conditions, and Model 3, which includes time delays in the dynamics to account for the time needed for information processing. Interestingly, the communication delay estimated from the data by using Model 3 (170 ms) is coherent with the typical delays in the action-perception loop, which includes anticipation, prediction, active preparation and muscular adjustments, in addition to passively added delays in the brain loops. Indeed, the sensorimotor control system requires coordinating different forms of sensory and motor data and these data are generally in various *formats*.

The Kuramoto model has already been successfully used in its simplest form to describe slowing down occuring in human group interaction, e.g., during applause (Néda et al., 2000). Authors of this work were able to explain the key features of applause dynamics but only exploiting parameters tuning. In our work, we propose model extensions to provide possible mechanisms underlying the observed slowing down, which emerges directly through the dynamics. Indeed, differently from the standard Kuramoto model, Models 2 and 3 are capable of capturing not only the observed synchronization level, but also the reduced frequency of oscillation compared to solo trials that we observed in our experiments on a group version of the mirror game. Our findings suggest, therefore, that the observed frequency reduction is due to both selective attention and time delays in the action-perception loop. Thus, both these phenomena should be appropriately taken into account when developing models of group synchronization, as for example in the extended Kuramoto models we propose in this paper. Therefore, we believe that this work represents a valuable contribution for the development of more robust models for the simulation of human group interaction, independent of parameter tuning.

The promising results reported in this manuscript call for further theoretical and experimental research in this area. For instance, from our experiments we could not discriminate which is the dominant effect between the selective attention and the information processing delays. Albeit Model 2 seems to be in average to perform better, we could not reject the hypothesis of equivalent performances with Model 3. Therefore, further experimental studies may be tailored to determine under which circumstances one factor may dominate the other and to assess whether the findings reported in this paper may extend to other kinds of alternative tasks. Finally, albeit our works focuses on steady-state behavior, since in this specific task the agents rapidly converge on their observed oscillation frequency, in other contexts transient dynamics may play a relevant role and should be further investigated.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repository. The name of the repository and accession number can be found below: https://github.com/diBernardoGroup/Modeling-frequency-reduction-in-human-groups-performing-a-joint-oscillatory-task.git.

ETHICS STATEMENT

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

MB, PD, and BB conceived the study. CC carried out the experiment through the software platform Chronos. CC and PD carried out the modeling and analytical investigations. All authors wrote the paper and reviewed the manuscript.

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When Visual Cues Do Not Help the Beat: Evidence for a Detrimental Effect of Moving Point-Light Figures on Rhythmic Priming

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Rhythm perception involves strong auditory-motor connections that can be enhanced with movement. However, it is unclear whether just seeing someone moving to a rhythm can enhance auditory-motor coupling, resulting in stronger entrainment. Rhythmic priming studies show that presenting regular rhythms before naturally spoken sentences can enhance grammaticality judgments compared to irregular rhythms or other baseline conditions. The current study investigated whether introducing a point-light figure moving in time with regular rhythms could enhance the rhythmic priming effect. Three experiments revealed that the addition of a visual cue did not benefit rhythmic priming in comparison to auditory conditions with a static image. In Experiment 1 (27 7–8-year-old children), grammaticality judgments were poorer after audio-visual regular rhythms (with a bouncing point-light figure) compared to auditory-only regular rhythms. In Experiments 2 (31 adults) and 3 (31 different adults), there was no difference in grammaticality judgments after audio-visual regular rhythms compared to auditory-only irregular rhythms for either a bouncing point-light figure (Experiment 2) or a swaying point-light figure (Experiment 3). Comparison of the observed performance with previous data suggested that the audio-visual component removed the regular prime benefit. These findings suggest that the visual cues used in this study do not enhance rhythmic priming and could hinder the effect by potentially creating a dual-task situation. In addition, individual differences in sensory-motor and social scales of music reward influenced the effect of the visual cue. Implications for future audio-visual experiments aiming to enhance beat processing, and the importance of individual differences will be discussed.

Keywords: rhythm, entrainment, rhythmic priming, audio-visual, auditory-motor, syntax, grammar, language

INTRODUCTION

The majority of research investigating rhythm processing (both perception and production) occurs in the auditory modality, as rhythm and beat processing are typically more precise and more frequent in the auditory domain (Grahn, 2012; Repp and Su, 2013; Comstock et al., 2018). However, attempts have been made to investigate whether regular visual information can effectively convey a rhythmic beat, both independently and in combination with auditory conditions. Research has shown that synchronization to visual stimuli with a visible movement trajectory (e.g., a tapping hand, a bouncing ball) is enhanced compared to discrete visual stimuli (e.g., flashing lights), and can reach the performance level of synchronization to auditory stimuli (Hove and Keller, 2010; Hove et al., 2013; Gan et al., 2015). Importantly, movement of the participant appears to be necessary to elicit equal performance between moving visual cues and auditory cues. Across different studies, bouncing balls (i.e., a moving visual stimulus) were superior to visual flashes (i.e., a static stimulus) and elicited similar performance to auditory stimuli (tones/beeps) in beat-based synchronization tasks, but not in beat-based perception tasks (Silva and Castro, 2016; Torres et al., 2019; Gu et al., 2020). These studies suggest that moving visual cues can match auditory stimuli only when the participant is engaged in a motor task (e.g., tapping synchronization), likely activating sensorimotor (visual-motor) networks (Gu et al., 2020).

Biological Motion and Beat Perception

As apparent movement (i.e., a bouncing ball) appears important to show a visual cue benefit for synchronization tasks, it is also possible that visual stimuli reflecting *body movement* (i.e., biological motion) might enhance the involvement of auditory-motor coupling in the brain, even without additional participant movement. The auditory-motor pathway (i.e., the connection between auditory and motor cortices) appears integral to beat perception and temporal prediction (Patel and Iversen, 2014; Morillon et al., 2015; Proksch et al., 2020; Cannon and Patel, 2021), as just *listening* to rhythms activates motor areas in the brain (Grahn and Brett, 2007; Chen et al., 2008; Gordon et al., 2018), and the motor system is actively involved in music perception (Maes et al., 2014). Studies have shown that adding participant movement to auditory stimuli can influence auditory perception (Phillips-Silver and Trainor, 2007; Brown and Palmer, 2012; Chemin et al., 2014; Mathias et al., 2015, 2016; Schmidt-Kassow et al., 2019), and actively engaging the motor system in beat-based processing, for example by tapping or moving along to a beat, enhances rhythm perception (Manning and Schutz, 2013). Further, participant pairs facing each other while synchronizing (flexing and extending knees) to an auditory metronome were more in-synch compared to when they were facing apart, a benefit attributed to the continuous visual cue of their partner (e.g., Miyata et al., 2017). However, limited research has investigated whether the addition of a biological motion visual cue without additional participant movement can enhance the auditory-motor loop and/or enhance perception.

Visual point-light figures have been shown to enhance auditory rhythm perception and synchronization. Su (2014b) used point-light figures (very similar to the ones used in our current study) that bounced in time with auditorily presented rhythms. Experiment 1 (n = 14) consisted of a same-different judgment task (i.e., beat-based perception) and Experiment 2 (n = 11 plus author) consisted of a synchronization task. Short, metrically simple rhythms [with five to seven intervals taken from Grahn and Brett (2007) and Grahn (2012)] were used. Rhythms were either presented alone (auditory condition) or with the point-light figure (audio-visual condition). In the same-different task, participants were presented with the same rhythm three times (with or without a point-light figure), and the third time they judged whether the third rhythm was the same or different. Participants performed better at the same-different task in the audio-visual condition compared to the auditory condition, suggesting a benefit of the point-light figure on rhythm perception. Similarly, in the synchronization task, participants were less variable in tapping to isochronous rhythms in the audio-visual condition compared to the auditory condition. For both experiments, auditory distractor sequences of different tempi were included that participants were told to ignore, but which made the task progressively more difficult. Interestingly, in both experiments, as performance in the auditory condition decreased, the effect of the visual stimulus increased, showing that the visual cue was only beneficial as the auditory rhythms became more difficult. In other words, the visual cue may have only been used when the beat was not easily extracted from the auditory stimulus.

However, other studies have not shown beneficial effects of visual biological motion (i.e., human movement or point-light figures portraying humans) on beat-based perception. Using the same visual point-light figures as Su (2014b) and short, weakly metrical sequences from Grahn and Brett (2007), Su (2014a) had participants perform a reproduction task (Experiment 1, n = 12 plus author) or a same-different task (Experiment 2, n = 19). In these experiments, the auditory (auditory rhythm), visual (point-light figure), or audio-visual (auditory and point-light figure) beat was provided for two beats before being presented simultaneously with the starting beat of the weakly metrical rhythms. Across both experiments, there was no benefit of the audio-visual condition compared to the auditory condition, showing that the visual cue did not help reproduction or differentiation of the weakly metrical sequences. Su (2014a) suggested that presenting the stimuli in multiple streams might have led to a high working memory load, which could have removed any effects of beat induction in the weakly metric rhythms. Additional studies in adults (Phillips-Silver and Trainor, 2007, 2008) and infants (Phillips-Silver and Trainor, 2005) showed that when participants bounced (or were bounced) with an ambiguous rhythmic sequence at either a duple (i.e., bounce every second beat) or triple (i.e., bounce every third beat) meter, their recognition of and liking for the unambiguous sequences of the same meter increased. However, passively watching an experimenter bouncing did not influence subsequent recognition (adults) or liking for (infants) unambiguous sequences in the meter that was bounced to, suggesting that beat-based perception alone was not affected by the visual cue. The literature is therefore conflicting as to whether adding a visual point-light animation without additional movement by the observer can aid auditory beat-based processing.

The current study investigated whether the addition of a moving point-light figure (i.e., with biological motion) could enhance beat-based perception within a rhythmic priming paradigm. Point-light animations are an interesting stimulus to study audio-visual movement as they have the potential to enhance the activation of auditory-motor connections in the brain. Just watching moving human point-light displays has been shown to activate the premotor cortex (Saygin et al., 2004; Saygin, 2007), and engage the mirror neuron system (Ulloa and Pineda, 2007; see also Copelli et al., 2021). Further, motor system activity is increased when participants are presented with actions that they can perform compared to those they cannot perform (Stevens et al., 2000), likely related to the strong link between action and action perception in the brain (Case et al., 2015). Additionally, human movement is typically perceived as more socially relevant and salient than object movement (i.e., bouncing balls) or non-human movement (i.e., moving horses) (Pyles et al., 2007; Pinto and Shiffrar, 2009). The ability of point-light animations to communicate biological movement is also shown in developmental studies. Children as young as 3-years-old can recognize point-light figures when they are moving but not when static, with ceiling recognition performance already at 5 years of age (Pavlova et al., 2001), and 12-month-old infants spontaneously follow the gaze direction of point-light figures (Yoon and Johnson, 2009). Such results suggest that point-light animations are adept at communicating human movement and social gestures. Taken together, such evidence suggests that watching a human point-light figure moving in a synchronous and physically plausible manner might strengthen the involvement of the auditory-motor connection in the brain during perception, thereby potentially enhancing participants' beat-based perception (as shown in Su, 2014b). Our aim was to recreate the beneficial conditions in Su (2014b) by using visual point-light animations and strongly metrical sequences to improve beat-based rhythm perception within a rhythmic priming paradigm.

Rhythmic Priming

A growing body of literature has shown that presenting a regular rhythmic prime before a set of naturally spoken sentences enhances grammaticality judgments for these sentences compared to irregular rhythmic primes or baseline conditions. A rhythmic priming effect has been shown for French speaking children (Przybylski et al., 2013; Bedoin et al., 2016; Fiveash et al., 2020), French speaking adults (Canette et al., 2019, 2020a), English speaking children (Chern et al., 2018) and Hungarian speaking children (Ladányi et al., 2021). This effect appears to be driven by a benefit to syntax processing after regular rhythms rather than a detrimental effect after irregular rhythms, as shown with environmental sounds, contemporary textural music, and silence as baseline comparison conditions (Bedoin et al., 2016; Canette et al., 2020b; Ladányi et al., 2021). Further, the effect appears specific to syntax processing rather than a general arousal effect, as no benefit of the regular rhythms was found for a non-linguistic control task (Chern et al., 2018; Ladányi et al., 2021) or a semantic evocation task (Canette et al., 2020b). These studies used longer rhythmic primes (17–32 s) compared to previous cueing studies (e.g., Cason and Schön, 2012; Cason et al., 2015; Falk and Dalla Bella, 2016) with the aim to globally entrain endogenous neural oscillations to the external regular rhythms.

Within the framework of dynamic attending theory (Large and Jones, 1999; Jones, 2018), the entrained neural oscillations should persist once the rhythm stops, enhancing the processing of the subsequently presented naturally spoken sentences. The strength of the entrained oscillations should determine how long the oscillation persists, with stronger driven oscillations persisting for a longer period of time after the end of the input, and less likely to be captured by new rhythms or events (Jones, 2018; Fiveash et al., 2020). Therefore, enhancing the entrainment to the regular rhythmic primes should also enhance the rhythmic priming effect, with stronger entrainment resulting in prolonged effects of the regular rhythmic primes on subsequent sentence processing. Previous research has shown that adding a motor component (tapping along or rhythmic training) to rhythmic cueing studies (i.e., with a one-to-one match of the cue and target as in Cason and Schön, 2012) can enhance the effect of the rhythmic cue on subsequent speech perception (Cason et al., 2015; Falk and Dalla Bella, 2016; Falk et al., 2017). However, to our knowledge, no studies have yet investigated whether rhythmic cueing or rhythmic priming can be enhanced with the addition of a visual cue in the absence of participant movement. Visual cues depicting human movement could be particularly valuable as they might lead to enhanced involvement of auditory-motor coupling and its related contribution to beat and meter processing.

Current Study

The current set of experiments aimed to investigate whether adding a visual point-light figure moving in time to regular rhythms could enhance the rhythmic priming effect by enhancing entrainment to the regular rhythms. Based on the links between point-light figures and motor activation in the brain (Saygin et al., 2004; Saygin, 2007), and the capacity of the point-light figures for enhancing beat-based processing for strongly metrical stimuli (Su, 2014b), we decided to create point-light figures similar to those used in Su (2014a,b) as our visual stimulus. However, as reviewed above, the evidence supporting beneficial effects of visual cues without additional movement from the participant is limited. Therefore, there are three possible outcomes for the following experiments comparing regular audio-visual primes to either regular auditory primes (Experiment1) or irregular auditory primes (Experiments 2 and 3). The first possible result pattern would reflect a *beneficial* effect of the visual cue on beat-based perception. In this case, regular audio-visual primes should result in improved grammaticality judgments compared to both regular auditory primes and irregular auditory primes. The second possible result pattern would reflect *no effect* of the visual cue on beat-based perception. In this case, grammaticality judgments should be equal after regular audio-visual primes and regular auditory primes, and still result in enhanced performance compared to irregular primes (i.e., the rhythmic priming effect). The third possible result pattern would reflect a *detrimental* effect of the visual cue on beat-based perception (i.e., linked to an additional information cost if not integrated with the auditory information). In this case, regular audio-visual primes should result in poorer grammaticality judgments compared to regular auditory primes, and the same or lower performance compared to irregular primes.

Experiment 1 was conducted with children and directly investigated whether adding a visual point-light figure *bouncing* in time to regular rhythms would enhance grammaticality judgments compared to the same regular rhythms presented only in the auditory modality. This experiment was therefore a direct test of whether the visual cue enhances rhythmic priming compared to the same cue without a visual component. To preface the results, Experiment 1 showed that the regular audio-visual rhythms resulted in *poorer* performance on the grammaticality judgment task compared to the regular auditory rhythms (supporting the detrimental effect hypothesis). We hypothesized that children were more likely to be distracted by the addition of a visual point-light figure and may have difficulties integrating the two types of information. They may have thus processed the stimuli as a dual-task rather than an integrated percept. Therefore, we ran Experiments 2 and 3 with adults.

Experiments 2 and 3 built more directly on the priming conditions initially used in previous studies (e.g., Przybylski et al., 2013; Chern et al., 2018; Fiveash et al., 2020), and thus consisted of regular audio-visual primes and irregular auditory primes. Irregular auditory primes were introduced to have a stronger contrast with the regular audio-visual primes and to investigate whether the regular audio-visual primes still elicited the rhythmic priming effect. To further investigate the role of the visual cue and in particular its benefit over a purely auditory regular rhythm, we compared these data to previous adult data using regular and irregular auditory rhythms without visual cues (Canette et al., 2019). The visual cue in Experiment 2 was the same bouncing point-light figure as in Experiment 1. To investigate whether the specific movement of the visual cue was important, the point-light figure in Experiment 3 was changed to a swaying figure which had more precise alignment of the hip movement to the beat onsets. None of the experiments showed a benefit of the regular audio-visual prime on grammaticality judgments, supporting previous research suggesting no benefit of purely visual cues on beat-based perception. On the contrary, the results indicated that the addition of the visual information reduced the typical rhythmic priming benefit, reflecting a detrimental effect of the visual cues. However, individual differences appeared to influence the impact of the visual cue and will be outlined below (including perspectives for conditions leading to potential benefits).

GENERAL METHOD

Design

All experiments were 2 (condition: audio-visual, auditory) by 2 (sentences: grammatical, ungrammatical) within-subject designs. Across all experiments, auditory rhythms were paired with a static visual image of the point-light figure so that they also contained visual information. In Experiment 1, children (aged 7–9 years) listened to regular rhythms presented simultaneously with a point-light figure that *bounced* in time with the underlying beat of the music, referred to as audio-visual rhythms (RegAV), or regular rhythms presented simultaneously with a static visual image, referred to as auditory rhythms (RegA). In Experiment 2, adults were presented with RegAV rhythms with the same bouncing point-light figure as in Experiment 1, or *irregular* auditory rhythms (IrregA) presented with the same static image. In Experiment 3, adults were presented with RegAV rhythms with a *swaying* point-light figure, or IrregA rhythms with the same static image. See **Figure 1**.

Each experimental block consisted of one rhythm (AV or A) followed by six sentences. Experiment 1 contained 16 blocks of one rhythm followed by six sentences, and Experiments 2 and 3 consisted of eight blocks of one rhythm followed by six sentences. Starting condition (AV or A) was counterbalanced across participants, and there were four blocks of the same presentation type in a row aiming to enhance the effect of condition. Two different sentence lists (1, 2) were counterbalanced across participants, and counterbalancing was designed in a way that four different sets of stimulus presentation were possible across participants: list 1 with AV first; list 2 with AV first; list 1 with A first; list 2 with A first. Each block of six sentences contained three grammatical and three ungrammatical sentences. Within these constraints, all music and speech stimuli were fully randomized.

Stimuli

Rhythms

The regular and irregular experimental rhythms were the same as those used in Fiveash et al. (2020), and were approximately 32 s long. Three additional rhythms (created by the same composer) were used for the training phase to familiarize participants with the bouncing/swaying figures. All rhythms were created with musical instrument digital interface virtual studio technology (MIDI VST) and contained various percussive and electronic sounds (i.e., bass drum, snare drum, tom-tom, cymbal). Regular rhythms had a 4/4 meter, and a tempo of 120 beats per minute (bpm). Irregular rhythms were created from the regular rhythms by re-arranging the events in time, so that the sequences were highly irregular, with no underlying meter or pulse. See **Supplementary Material** for examples of the regular and irregular rhythms, as well as the Supplemental Information in Canette et al. (2019) for more rhythmic examples.

Point-Light Animations

For the audio-visual condition (RegAV), point-light animations were created using an infrared-based motion capture system (Qualisys Oqus 5+, 8 cameras, Qualisys Track Manager 14 software). To create the figures, a musically trained female was equipped with 28 reflective markers and bounced up and down (for bouncing stimuli, Experiments 1 and 2) or swayed side to side (for swaying stimuli, Experiment 3), with the knee flexion (bouncing) or hip extension (swaying) aligning with each beat. Movement was recorded at a frame rate of 120 frames per second, labeled, and exported to Matlab 2017b. Subsequently, markers were reduced to 20 joints (to avoid redundancies and create a clearer image, for more information on this procedure, see Burger et al., 2013), and rendered as .mov videos on a white background with black connectors between the points. To enhance the bouncing motion and to make knee movement clear, the point-light figure was rotated 45° to the left (when facing the figure) in the bouncing AV condition. For swaying, the point-light figure was facing forward, allowing for better viewing of the movement. The audio was added using QuickTime Player, v.10, ensuring correct (i.e., natural and aligned) synchronization

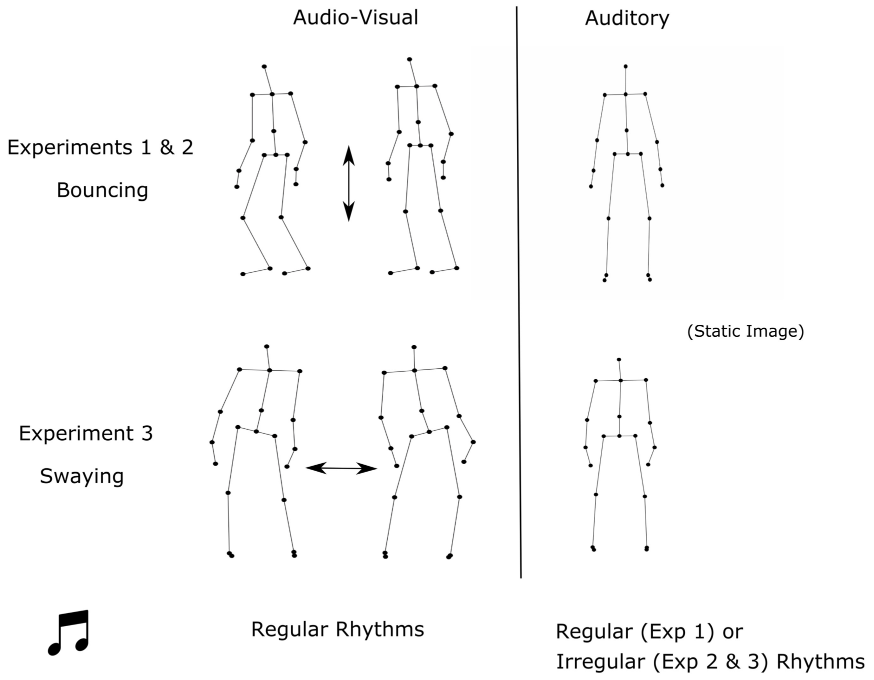

FIGURE 1 | Diagram showing the audio-visual (AV) and auditory conditions for the rhythmic priming experiments. The AV condition in Experiments 1 and 2 consisted of a bouncing figure that bounced up and down in time with the music. In Experiment 3 the AV condition consisted of a swaying figure that swayed side to side. The AV condition consisted of regular rhythms for all experiments, whereas the auditory condition consisted of regular rhythms in Experiment 1 and irregular rhythms in Experiments 2 and 3.

between rhythm and movement. See **Supplementary Material** for example animations. For the auditory conditions, a forward-facing static image of the same point-light figure was presented on the screen to control for effects of visual information between conditions. In a training phase before the experimental phase, participants were presented with in-synch and out-of-synch moving figures. To create the out-of-synch videos, the point-light figure was sped up to bounce at 160 bpm, and so looked particularly out-of-synch with the rhythm at 120 bpm (this was also confirmed in the pilot experiment presented below).

Sentences

Different sentences were used for the child experiment (Experiment 1) and the adult experiments (Experiments 2 and 3) based on different required difficulty levels. The child sentences consisted of two lists of 96 French sentences spoken naturally by a native French speaker and used in Fiveash et al. (2020). Each list contained 48 grammatical and 48 ungrammatical sentences that were matched on lexical properties, including number of words, number of syllables, and lexical frequency. Sentences that were grammatical in List 1 were ungrammatical in List 2, to ensure no effect of individual sentences. There were eight types of grammatical error: number (No), person (Pe), gender (Ge), tense (Te), auxiliary (Au), morphology (MS), position (Po), and past participle (PP). Eight sentences each were composed of the four main error types (No, Pe, Ge, and Te), and four sentences each were composed of the secondary error types (Au, MS, Po, and PP). Within each block of six sentences, there were always three grammatical and three ungrammatical sentences. The three ungrammatical sentences always included two different main error types, and one secondary error type. Further details and a list of all sentences can be found in Fiveash et al. (2020), and example sentences are presented in **Supplementary Table 1**.

The adult sentences (Experiments 2 and 3) were those used in Canette et al. (2019). The same creation of lists was conducted as in Experiment 1: the incorrect sentences were derived from correct sentences and separated into different lists, so participants did not hear the same sentence in both its correct and incorrect form. Sentences in each list were matched for number of words, number of syllables, and for lexical frequency. In this stimulus set, each list contained 48 sentences (24 grammatical, 24 ungrammatical). Grammatical errors were morpho-syntactic (including tense, preposition, and person agreement errors) and subtle to increase difficulty for the adults. More details and the full stimulus set can be found in Canette et al. (2019); example sentences are presented in **Supplementary Table 1**.

Experiment 1 had more sentences (and therefore experimental blocks) than Experiments 2 and 3 because it was possible to include more diverse syntactic errors for children, as they do not perform at ceiling level on grammaticality tasks. For adults, creating syntactic errors that are subtle and do not result in ceiling or floor effects is challenging, limiting the number of sentences available. We here used available stimuli from Canette et al. (2019) that had shown a rhythmic priming effect in adults previously.

Training Phase

To enhance the auditory-motor link, a training phase was introduced to engage participants with the experiment and to familiarize them with the concept of synchronization. In the training phase, participants were told that they would see two different dancers. The first dancer was introduced as a *good* dancer. The good dancer was always in-synch with the music, and consisted of black dots on a white background, as in the main experiment. Participants were told that they could move along with the dancer if they wanted to. The second dancer was introduced as a *bad* dancer who would try to imitate the good dancer. The bad dancer was presented with white dots on a black background to emphasize the difference from the good dancer. Participants saw videos of both dancers. It was explained that participants would see the good dancer followed by the bad dancer, and they had to judge whether the bad dancer did a good job of imitating the good dancer or not. There were four trials, and after each trial, participants verbally indicated to the experimenter whether the bad dancer imitated the good dancer well or not. Half of the time the bad dancer was out-of-synch with the good dancer, and half of the time the bad dancer was in-synch with the good dancer. If the participant indicated the wrong answer, the experimenter explained why the bad dancer was doing a good or bad job of copying the good dancer. All training videos were 8 s long, corresponding to one cycle of the experimental rhythms.

Individual Differences Tests

To investigate whether individual differences were related to performance after audio-visual or auditory primes, we measured reading age of children (RA), and administered the Barcelona Musical Reward Questionnaire (BMRQ; Mas-Herrero et al., 2013) to adults. Children completed a French age-normed reading measure, the Test de l'Alouette (Lefavrais, 1967), also used in Fiveash et al. (2020). The Test de l'Alouette is a pure measure of reading age (RA), as semantic prediction of the text is largely impossible. Each child had 3 min to read this text out loud. Their score was based on their reading speed (i.e., how much of the text they were able to read) and number of mistakes made, which were then compared to the normed values to calculate RA. Their chronological age (CA) was also recorded. RA was measured for children as previous research has shown connections between RA and the effects of regular rhythmic primes (Fiveash et al., 2020).

Adults completed the French translation of the BMRQ (Saliba et al., 2016), which contains 20 questions corresponding to the sub-scales: musical seeking, emotion evocation, mood regulation, social reward, and sensory-motor. Normed values were calculated at http://brainvitge.org/z_oldsite/bmrq.php. RA or equivalent baseline grammar tests were not implemented for adults, as the population was largely young University students without speech or language disorders who were expected to be relatively homogenous in their reading and grammar level. Music reward was not measured for children as the questions and norms were directed toward an adult audience with more experience in music listening. Children were informally asked whether they had music lessons, but considering the young age range, the small number of years (or months) of music training reported by some children was not analyzed. Both RA (measured in children) and musical reward (measured in adults) were expected to relate to the rhythmic priming effect. More specifically, children with higher RAs were expected to show a rhythmic prime benefit (Fiveash et al., 2020), and perhaps be more positively affected by the audio-visual primes, and adults with higher musical reward (particularly in relation to the sensory-motor sub-scale) were expected to perform better after the audio-visual regular primes compared to the auditory irregular primes, as they were more likely to be engaged with the rhythmic stimuli.

Procedure

The procedure was similar for all participants, but was adapted depending on age. Children were tested in a quiet room with an experimenter who sat with the child throughout the experiment to ensure adherence to the task and to launch each trial. Adults were tested in a sound-proof booth and progressed through the experiment by themselves. Both children and adults completed the training phase. At the end of the training, the experimenter explained that in the experiment only the good dancer would be dancing, and that sometimes the dancer would be "in form" and dancing, but at other times the dancer would be tired from all the dancing and needed to take a rest. Participants were told that they could move too when the dancer was dancing, but that when the dancer was resting, they should stop moving and listen carefully to the music. They were also told that after the music stopped, they would hear several sentences. For children, it was described that the sentences would either be spoken by a dragon who was always right (correct dragon), or a dragon who was always wrong (confused dragon). Pictures of both dragons were shown next to each other on the screen, and participants heard an example sentence. It was emphasized that the errors would be French errors, not errors of content (e.g., if the dragon said it was snowing outside, but it was not, this would not be an error). For adults, it was described that the sentences would be either grammatically correct or incorrect. After ensuring the participant understood the task, the experimental phase started. For each block, a rhythm (with either a concurrent bouncing/swaying point-light figure or a static point-light figure) was played for 32 s, followed by six sentences presented with the pictures of the dragons (or the words correct/incorrect for adults) on the screen. At the end of each sentence, children indicated whether the clever dragon or the confused dragon had spoken the sentence. Adults indicated whether the sentence was grammatically correct or incorrect. Participants could indicate that there was an error before the end of the sentence. In this case, the dragons (or words correct/incorrect) disappeared from the screen, but the sentence continued until the end. For children, the experimenter pressed a button to continue once the child was ready for the next sentence, and adult participants progressed by pressing the spacebar. After each block, participants were told whether the dancer would dance or whether the dancer needed to take a break in the next block. There was a break after every two blocks. The experiments were run on MacBook Pro laptops, using Matlab (version 2018a) and Psychtoolbox (version 3.0.14).

At the end of the experiment, children completed the Test de l'Alouette individually, and adults completed the BMRQ. The full experiment (including the training phase) took approximately 24 min for children and 12 min for adults. Children were encouraged throughout the experiment and given pauses every two blocks to ensure attention.

Validation of Synchronized Stimuli

To ensure that the experimental videos were perceived as being in-synch with the rhythms, and to ensure that the practice videos were perceived as either in- or out-of-synch as expected, a pilot test was run on eight adult participants with the bouncing stimuli. Participants rated synchronization of the point-light figure with the rhythm on a scale from 1 (very unsynchronized) to 10 (very synchronized). All experimental videos were presented first (randomized for each participant) to ensure they were not influenced by the out-of-synch videos, followed by the practice videos (randomized). Practice videos consisted of three *in-synch* point-light figures with a white background, three *in-synch* point-light figures with a black background, and three *out-of-synch* point-light figures with a black background.

The four experimental rhythms were rated as highly in-synch (M_{range}: 7.25–8.13, SD_{range}: 1.60–2.25). For the practice videos, the three out-of-synch practice videos were rated as highly out-of-synch (M_{range}: 2.38–2.63, SD_{range}: 1.30–1.51). The in-synch practice videos were generally also rated as in-synch, but had more varied ratings (M_{range}: 6.5–8.13, SD_{range}: 1.13–2.27). These data confirmed that the experimental videos were perceived as sufficiently in-synch for the purpose of the experiment, and that the distinction between in-synch and out-of-synch point-light figures was clear for the practice trials.

Analysis

Power Analysis and Sample Size

Sample sizes were determined based on previous rhythmic priming studies which found significant benefits of regular compared to irregular primes. Specifically, previous behavioral sample sizes for typically developing children and adults performing the rhythmic priming task have ranged from $n = 16$ to $n = 35$, with the ability to detect small to medium effect sizes (Canette et al., 2019, $n = 25$, $d = 0.37$; Canette et al., 2020b, $n = 30$, $\eta_p^2 = 0.30$; Chern et al., 2018, $n = 16$, $d = 0.57$; Fiveash et al., 2020, Experiment 2, $n = 35$, $d = 0.33$; Ladányi et al., 2021, $n = 17$, $d = 0.36$). We therefore aimed to follow these conventions and tested approximately 30 participants for each experiment, resulting in 27 children in Experiment 1 (based also on classroom recruitment possibilities), and 31 adults in Experiments 2 and 3.

Signal Detection

Detection of grammatical errors was measured by calculating *d* prime (*d*') from signal detection theory (Stanislaw and Todorov, 1999). D prime provides a measure of sensitivity to the signal which considers both hits (i.e., when there was an error and the participant indicated that there was an error) and false alarms (i.e., when there was no error, but the participant indicated that there was an error). The *d*' value is created by subtracting the *z*-score of the false alarms from the *z*-score of the hits. Extreme hit or false alarm values of one (i.e., 100%) or zero (i.e., 0%) were corrected to 0.99 or 0.01 respectively, as suggested in Stanislaw and Todorov (1999). A measure of response bias (response bias *c*) was also calculated by multiplying the sum of the *z*-scores for hits and false alarms by –0.50. Values above zero suggest a bias to respond grammatical, whereas values below zero suggest a bias to respond ungrammatical.

Statistical Analyses

Paired-samples *t*-tests were used for each experiment to judge whether *d*' values and response bias *c* values differed depending on prior presentation of an audio-visual rhythmic prime (RegAV for all experiments) or an auditory rhythmic prime (RegA for Experiment 1 and IrregA for Experiments 2 and 3). Response bias *c* values were also compared to 0 using one-sample *t*-tests.

The adult data in Experiments 2 and 3 were directly compared to previously published data in Canette et al. (2019), who reported a benefit of the regular compared to irregular rhythmic primes on subsequent grammaticality judgments. Canette et al. (2019) used the same rhythmic primes, the same sentences, and the same design as Experiments 2 and 3. Further, both participant groups consisted of adults of a similar age (in Canette et al., 2019: $n = 25$, $M_{age} = 21.2$ years, $SD = 1.76$; range = 19–26). The only differences between the two experiments were that (a) the current experiments included an audio-visual manipulation, and (b) the current experiments presented four of the same prime types in a row (e.g., AAAA BBBB) whereas the previous experiment alternated every two blocks (e.g., AA BB AA BB). To investigate the effect of the visual-cue on performance, independent-samples *t*-tests were conducted to compare (a) performance after RegAV primes in Experiments 2 and 3 to performance after RegA primes in Canette et al. (2019), and (b) performance after IrregA primes in Experiments 2 and 3 compared to the same IrregA primes in Canette et al. (2019)[1]. Respectively, these comparisons allowed us to investigate the effect of adding a visual cue to the regular prime, and to observe whether performance after irregular primes stayed consistent across the experiments. All analyses were run in R studio (R Core Team, 2018).

Individual Differences

For Experiment 1, spearman correlations were calculated for RA and CA for each condition (RegAV and RegA). Holm–Bonferroni adjusted *p*-values (*p*') are presented after correcting for multiple comparisons. These correlations were run separately (i.e., not on the difference score), as we expected a correlation with both RegAV and RegA, based on Fiveash et al. (2020). For Experiments 2 and 3, multiple regressions were run on the difference score of the conditions (RegAV minus IrregA) to investigate whether the sub-scales of the BMRQ were related to the direction of the rhythmic priming effect. The difference score represents the strength of the rhythmic priming effect, and in the current experiments specifically, the strength of the regular audio-visual primes compared to the irregular auditory primes. Values greater

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[1] A 2 × 2 mixed ANOVA was not run because there was no IrregAV condition. Therefore, we directly tested the contrast of interest (RegAV vs. RegA), and we additionally tested whether there was a difference in "baseline" (auditory only) irregular performance (IrregA vs. IrregA) between the two experiments.

than 0 indicate a benefit of the RegAV primes, whereas values less than 0 indicate a benefit of the IrregA primes. We report first the standard regression model (with all sub-scales included: musical seeking, emotion evocation, mood regulation, social reward and sensory-motor), and then the backward stepwise regression model for comparison. Backward stepwise regression (where all sub-scales are included at first, and then those which contribute the least are iteratively removed until there is a model with only significant predictors) was chosen to explore whether the standard model was missing important predictors. We chose backward stepwise regression as it is considered more robust to suppressor effects compared to forward regression (Field et al., 2012).

EXPERIMENT 1

Participants

Twenty-seven children aged between 7 and 9 years of age (M = 95.26 months, SD = 3.94 months, range: 90 months–101 months; 7 years, 6 months–8 years, 5 months) from "CE1" grade of a public French school in Lyon, France, participated in this experiment. Informed consent was provided by the parents, and the experiment was run in accordance with the Declaration of Helsinki.

Results and Discussion

D Prime

The paired-samples t-test showed that sensitivity to grammatical errors was significantly worse after a RegAV prime (M = 1.94, SD = 1.05) compared to a RegA prime (M = 2.19, SD = 1.02), $t(26) = 2.09$, $p = 0.047$, $d = 0.40$. See **Figure 2A**. These data show that adding bouncing point-light figures to the regular rhythms significantly reduced performance compared to the regular rhythms alone.

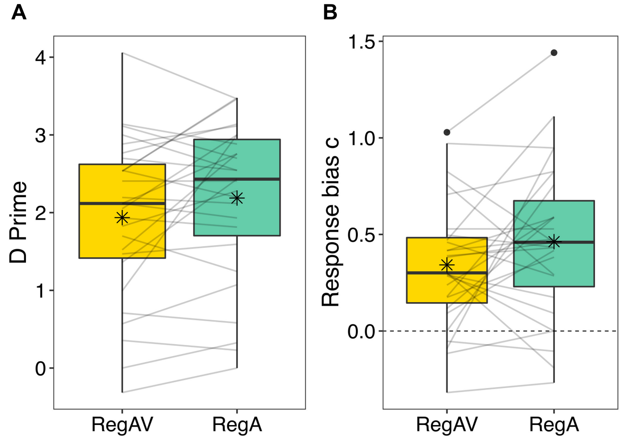

FIGURE 2 | D prime **(A)** and response bias c **(B)** values after regular audio-visual (RegAV) primes and regular auditory (RegA) primes. Individual lines represent individual participant data, and means are represented with a black asterisk. The dotted line for response bias c refers to the point of no bias. Boxplots represent the distribution of data as implemented in ggplot2 in R (R Core Team, 2018), with the black line representing the median, the box representing the interquartile range, the whiskers presenting the spread of data, and extra points representing potential outliers.

Response Bias c

The difference in response bias c was not significant depending on condition, $t(26) = 1.68$, $p = 0.11$, as participants were biased to respond grammatical in both the RegAV condition (M = 0.34, SD = 0.33), $t(26) = 5.41$, $p < 0.001$ and the RegA condition (M = 0.46, SD = 0.40), $t(26) = 5.94$, $p < 0.001$. See **Figure 2B**.

Reading and Chronological Age

Reading age (in months) was positively correlated with performance after both the RegAV, $r(25) = 0.46$, $p = 0.015$, $p' = 0.03$ and RegA, $r(25) = 0.398$, $p = 0.04$, $p' = 0.079$ primes (**Figure 3A**); however, CA was not [RegAV: $r(25) = 0.18$, $p = 0.37$; RegA: $r(25) = 0.037$, $p = 0.85$], **Figure 3B**. After correction for multiple comparisons, the correlation between RA and RegA was no longer significant, while the correlation with RegAV remained significant, indicating a slightly stronger correlation[2] with RA when a visual cue was present.

Experiment 1 showed a detrimental effect of the visual point-light animation on grammaticality judgments, with reduced sensitivity to grammaticality judgments after RegAV primes compared to RegA primes. One possibility to explain this result is that children were disturbed or distracted by the point-light figure, especially with hearing both audio-visual and auditory versions of the same regular rhythms. It is also possible that the visual cue may have become costful and created a dual-task situation, rather than facilitating beat extraction and entrainment. To investigate whether the point-light figure was costful only for children, we conducted a new experiment with adults and compared regular audio-visual and irregular auditory rhythms.

EXPERIMENT 2

Participants

Thirty-one adults (28 women, three men; M_{age} = 20.97 years, SD = 2.98; range = 19–35) participated in Experiment 2. All were native French speakers and were recruited through the University of Burgundy. On average, participants had 1.69 years (SD = 2.73, range = 0–9) of musical experience. Fifteen participants reported some musical experience (seven were still practicing at the time of testing), and 16 participants reported no musical experience. The participants with musical training had an average of 3.5 years (SD = 3.04) of courses and playing, ranging from 1 month to 9 years. Eighteen participants reported attending dance classes in the past, and four attended dance classes at the time of testing. One participant reported being dyslexic, and no participants reported a history of neurological, hearing, or vision issues. All participants provided written informed consent, and the study was approved by the French ethics committee (*Comité de*

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[2] Though note that a Fisher z test showed no significant difference between the correlations, $z = 0.44$, $p = 0.33$.

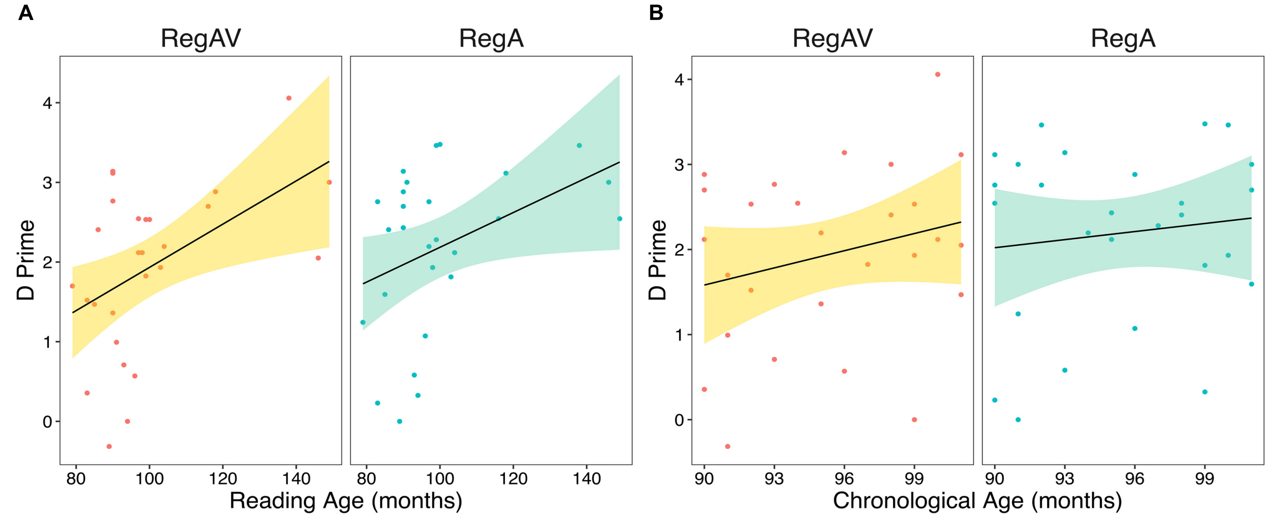

FIGURE 3 | Correlations between d prime performance after regular audio-visual (RegAV) rhythms and regular auditory (RegA) rhythms for **(A)** reading age and **(B)** chronological age. Individual dots represent individual participants. Shaded error bars represent one standard error of the mean, regression line fitted with a linear model in R.

Protection des Personnes, Ile de France X, CPP). Participants were given course credit for their participation.

Results and Discussion

D Prime

The paired-samples t-test showed that there was no significant difference between performance after RegAV primes (M = 1.92, SD = 1.07) compared to IrregA primes (M = 2.07, SD = 0.84), $t(30)$ = 0.73, p = 0.47. This result was surprising, as irregular rhythms typically result in poorer performance on grammaticality judgments compared to regular rhythms (Przybylski et al., 2013; Bedoin et al., 2016; Chern et al., 2018; Canette et al., 2019, 2020a; Fiveash et al., 2020; Ladányi et al., 2021). To investigate whether the addition of a bouncing figure was detrimental to subsequent performance, we compared the present results to the results of Canette et al. (2019), see **Figure 4**. The between-subjects analysis showed that performance after the RegAV condition of the present experiment was reduced compared to performance in the RegA condition of Canette et al. (2019), $t(54)$ = 1.96, p = 0.054, d = 0.53, even though this difference just fell short of significance. There was no difference in performance after irregular primes in the present experiment (IrregA) compared to after irregular primes (IrregA) in Canette et al. (2019), $t(54)$ = 0.06, p = 0.96. The comparison of these two datasets suggests that the addition of an audio-visual bouncing figure removed the benefit of the regular rhythmic primes.

Response Bias c

The paired-samples t-test showed no difference between the two conditions for response bias c, $t(30)$ = 0.26, p = 0.80, as both RegAV (M = 0.53, SD = 0.49), $t(30)$ = 6.05, p < 0.001, d = 1.09 and IrregA (M = 0.51, SD = 0.44), $t(30)$ = 6.50, p < 0.001, d = 1.17 showed a significant bias to respond grammatical. Between-subjects, there were no differences in response bias for RegAV compared to RegA, $t(54)$ = 0.05, p = 0.96 in Canette et al. (2019), or between the two irregular auditory conditions, $t(54)$ = 0.54, p = 0.59.

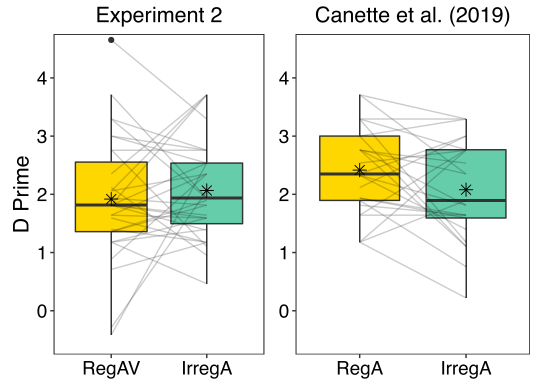

FIGURE 4 | Comparison of the current audio-visual (AV) experiment (Experiment 2; audio-visual regular primes: RegAV, auditory-only irregular primes: IrregA) compared to the experiment from Canette et al. (2019), n = 25 (auditory-only regular primes: RegA, auditory-only irregular primes: IrregA). Regular and irregular rhythms were identical in both experiments; however, in Experiment 2, a bouncing figure was added to the regular rhythms, and a static image of this same figure was added to the irregular rhythms. Boxplots represent the distribution of data as implemented in ggplot2 in R (R Core Team, 2018), with the black line representing the median, the box representing the interquartile range, the whiskers presenting the spread of data, and extra points representing potential outliers. Individual lines represent individual participant data, and the asterix represents the mean.

Barcelona Musical Reward Questionnaire

The multiple linear regression model showed that the difference score of RegAV minus IrregA was not predicted by any of the sub-scales of the BMRQ (all p-values > 0.10), and that the model was not significant, $F(5,25) = 1.96$, $p = 0.12$, with an r^2 of 0.28 (adjusted $r^2 = 0.14$). However, the backward stepwise model showed that the sensory-motor sub-scale was a significant negative predictor of the difference score (Estimate = −0.03, $t = -2.08$, $p = 0.047$), and the model including the sensory-motor sub-scale and the mood regulation sub-scale (Estimate = −0.03, $t = -1.39$, $p = 0.17$) was significant, $F(2,28) = 4.77$, $p = 0.02$, $r^2 = 0.25$, adjusted $r^2 = 0.20$. The negative contribution of the sensory-motor scale (i.e., how strongly does music induce body movements within individuals) suggests that participants' sensory-motor sensitivity may predict how they are affected by the bouncing figure. Those with *low* sensory-motor scores performed *better* after the bouncing figure, whereas those with *high* sensory-motor scores did *worse* after the bouncing figure. It is possible that participants with low scores were aided by the bouncing figure to extract the beat, whereas those who already had high sensory-motor sensitivity were more distracted by the figure, or aligned themselves to different aspects of the bouncing figure (e.g., the hands, which were not necessarily fully aligned with the beat).

The results of Experiment 2 provide further evidence for a detrimental effect of the point-light figures on grammaticality judgments. However, considering that the bouncing movement was aligned to the knee flexion, and the other body parts were not controlled (i.e., they were naturally moving so could have created antiphase or unsynchronized movements), we decided to change our point-light figure movement to a swaying figure, with clear and precise hip movements aligned with the beat. The swaying movement also allowed the figure to be forward-facing, which may have been important to the perception of the figure as a person.

EXPERIMENT 3

Participants

Thirty-one native French speaking adults participated in Experiment 3 ($M_{age} = 20$ years, $SD = 1.9$; range = 18–26; 26 women) and were recruited from Universities in Lyon and social media. On average, participants had 3.61 years ($SD = 4.24$; range = 0–13) of musical experience (including years of classes and years of individual playing). Nineteen participants reported that they had previously played music ($M = 5.89$ years, $SD = 3.97$, range = 1–13), and eight reported to currently play music. Seventeen participants reported attending dance classes in the past, and two currently attended dance classes. Participants reported no history of dyslexia or neurological issues, and no issues with hearing or vision that precluded them from participating in the study. All participants provided written informed consent, as approved by the French ethical committee (*Comité de Protection des Personnes Ile de France X, CPP*). They were paid 12 euros an hour for their participation.

Results and Discussion

D Prime

The paired-samples t-test showed no significant difference in performance after RegAV primes ($M = 2.34$, $SD = 0.88$) compared to IrregA primes ($M = 2.48$, $SD = 0.90$), $t(30) = 0.82$, $p = 0.42$ in the current experiment. Between-subjects, there was no significant difference in performance after RegAV primes in the current experiment compared to the RegA primes in Canette et al. (2019), $t(54) = 0.33$, $p = 0.74$. However, compared to the IrregA condition in Canette et al. (2019), performance after the IrregA condition in the current audio-visual experiment appeared somewhat higher, though not significantly, $t(54) = 1.69$, $p = 0.10$ (**Figure 5**).

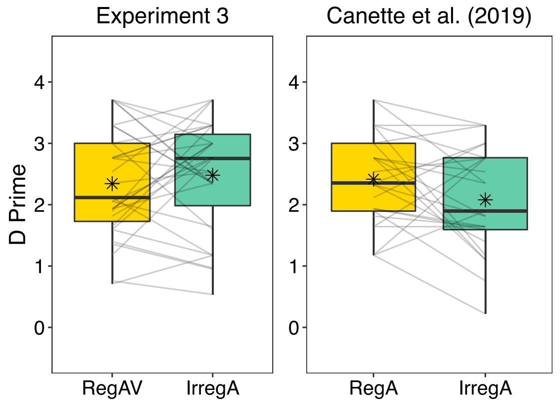

FIGURE 5 | Comparison of the current audio-visual (AV) experiment (Experiment 3; audio-visual regular primes: RegAV, auditory-only irregular primes: IrregA) compared to the experiment from Canette et al. (2019), $n = 25$ (auditory-only regular primes: RegA, auditory-only irregular primes: IrregA). Regular and irregular rhythms were identical in both experiments; however, in Experiment 3, a swaying figure was added to the regular rhythms, and a static image of this same figure was added to the irregular rhythms. Boxplots represent the distribution of data as implemented in ggplot2 in R (R Core Team, 2018), with the black line representing the median, the box representing the interquartile range, the whiskers presenting the spread of data, and extra points representing potential outliers. Individual lines represent individual participant data, and the asterix represents the mean.

Response Bias c

There was no significant difference between conditions, $t(30) = 0.64$, $p = 0.53$. Participants were significantly biased to respond grammatical in both the RegAV ($M = 0.54$, $SD = 0.46$), $t(30) = 6.52$, $p < 0.001$, $d = 1.17$ and the IrregA ($M = 0.61$, $SD = 0.32$), $t(30) = 10.71$, $p < 0.001$, $d = 1.92$, conditions. There were also no significant differences in response bias for RegAV compared to RegA, $t(54) = 0.05$, $p = 0.96$ in Canette et al. (2019), or between the two irregular auditory conditions, $t(54) = 1.61$, $p = 0.11$.

Barcelona Musical Reward Questionnaire

The multiple linear regression model showed that the difference score of RegAV minus IrregA was negatively predicted by the sensory-motor sub-scale (Estimate = −0.06, $t = -2.78$, $p = 0.01$). The social reward sub-scale was approaching significance (Estimate = 0.03, $t = 1.73$, $p = 0.096$), and no other sub-scales were significant (all p-values > 0.46). However, the model itself did not reach significance, $F(5,25) = 2.18$, $p = 0.09$, with an r^2 of 0.30 (adjusted $r^2 = 0.16$). The backward stepwise model with two sub-scales was significant, $F(2,28) = 4.67$, $p = 0.02$,

r^2 = 0.25, adjusted r^2 = 0.20: it confirmed that the sensory-motor sub-scale was a significant negative predictor of the difference score (Estimate = −0.05, t = −2.59, p = 0.01), and that the social reward sub-scale was a positive predictor of the difference (Estimate = 0.04, t = 2.63, p = 0.01). Taken together, these results support the results from Experiment 2 (bouncing figure), that participants with low sensory-motor sensitivity performed better after watching the swaying figures, but that participants with high sensory-motor sensitivity performed worse after watching these figures. Additionally, the positive social reward sub-scale predictor suggests that participants who scored *higher* on the social reward sub-scale (i.e., related to the social bonding aspect of music) also performed *better* after the audio-visual rhythms. The swaying figure was facing directly toward the participants, compared to the bouncing figure, which was facing to the side. It is possible that watching another "person" swaying in time to the rhythms may have aided the participants who had high social reward from music in extracting the beat.

GENERAL DISCUSSION

Across three experiments in children (Experiment 1) and adults (Experiments 2 and 3) we found that adding a visual cue in the form of a point-light figure bouncing (Experiments 1 and 2) or swaying (Experiment 3) to a regular rhythmic prime did not enhance subsequent grammaticality judgments of naturally spoken sentences. There was evidence to suggest that the addition of this visual figure instead removed the typically observed benefit of the rhythmic prime, and was detrimental to beat-based perception. Interestingly, individual differences appeared to affect how the visual cue influenced the participants. As RA in children increased, they performed better after both the regular audio-visual primes and the regular auditory primes compared to children with lower RAs; however, this effect remained significant after multiple comparison correction only for the grammaticality judgments after RegAV primes. In both Experiments 2 and 3, adults who scored lower on the sensory-motor subscale of the BMRQ appeared to be aided by the visual cue (better performance after RegAV compared to IrregA primes), whereas those who scored higher on this scale performed worse after the RegAV primes. Additionally, for the swaying figure of Experiment 3, participants with higher social scores on the BMRQ performed better after the RegAV prime compared to the IrregA prime.

Detrimental Effect of Visual Cue on Grammaticality Judgments

The current results suggest that adding a visual cue to a regular rhythmic prime reduces the beneficial effect of the prime compared to regular primes presented only auditorily. In Experiment 1, children performed significantly worse on the grammaticality task after a RegAV prime compared to a RegA prime, directly showing that the addition of a point-light bouncing figure reduced the effect of the prime on performance. In Experiments 2 and 3, adults were presented with RegAV and IrregA primes. No differences were found between these two conditions in either experiment. However, considering the typical finding of a beneficial effect of the regular compared to irregular primes, we compared these results to the pure auditory experiment of Canette et al. (2019). In Experiment 2, between-subjects analyses showed that performance in the RegAV condition was reduced in comparison to the RegA data in Canette et al. (2019), while the IrregA condition was comparable to performance with the same primes in Canette et al. (2019). These results suggest that for adults, the addition of the visual cue reduced the beneficial effect of the regular prime. The between-subjects comparison was inconclusive for Experiment 3, with no difference between RegAV and RegA or between IrregA and IrregA when compared to Canette et al. (2019).

Together with previous findings, the current results suggest that passively watching a visual point-light figure does not necessarily enhance rhythm and beat processing. Previous research involving a cueing component showed that including auditory-motor manipulations seem to enhance the processing of the rhythm (e.g., Cason et al., 2015; Falk and Dalla Bella, 2016; Falk et al., 2017). However, visual cues without additional movement from the participant have shown mixed effects on rhythm processing (positive: Su, 2014b; no effects: Phillips-Silver and Trainor, 2005, 2007; Su, 2014a), and the positive effects were shown for a same-different task and a synchronization task with small sample sizes (14 and 11 plus author, respectively; Su, 2014b). To our knowledge, the current experiments were the first to add a moving point-light figure to a rhythmic priming experiment. Our aim was to use the moving point-light figures to enhance the activation of the auditory-motor connection in the brain (Saygin et al., 2004; Saygin, 2007), thereby improving rhythmic entrainment and enhancing subsequent sentence processing. Instead, the visual figure appeared to remove the benefit of the regular rhythm, suggesting weaker entrainment to the rhythm and/or disturbing effects due to the additional visual information.

The addition of the visual point-light animation may have reduced or interrupted rhythmic entrainment. For example, the extra visual information may have been distracting to participants, especially if it was perceived as an additional source of beat-based information that was not integrated with the rhythm. Su (2014a) discussed the potential extra demands of adding a visual cue on working memory capacity, which may have removed potential beneficial effects of an extra cue to processing the beat. It is possible that the visual cue and auditory information were not integrated in the current experiment, even though the visual figures were synchronizing to the rhythm of the musical prime, with the goal to encourage an integrated audio-visual percept.

The potential effect of a visual cue might also depend on the task involved and the implementation of the cue, and it is possible that the rhythmic priming paradigm does not benefit from a visual cue under the current circumstances. The successful use of a moving point-light figure in Su (2014b) included a same-different task and a synchronization task, whereby the point-light figure continued to bounce during the tasks (e.g., in the final rhythm for the same-different task and during the synchronization task). In contrast, a rhythm reproduction task (with an accompanying visual figure during perception, but no accompanying visual figure during the reproduction phase) and a same-different task on weakly metrical rhythms did not show an effect of the visual cue (Su, 2014a). Watching a visual cue for 2 min without moving along also did not influence recognition of test sequences in the trained meter, suggesting that for longer stimuli, visual cues alone do not influence beat perception (Phillips-Silver and Trainor, 2005, 2007). Further, even with auditory-motor training (without a visual cue), Cason et al. (2015) did not show an improvement after the matching cue, but rather reduced performance on *mismatching* cues. It therefore appears that the effectiveness of a visual cue (here, a point-light figure) depends strongly on the type of stimuli, the task, and possibly the stimulus duration (i.e., perhaps participants paid less attention to the cue over time). The current rhythms were complex in the sense that they contained multiple instruments; however, the beat was clear and isochronous throughout a long timeframe whereby the same cycle was repeated for 32 s, making it relatively easy to extract the beat. It is therefore interesting to investigate individual differences that might be expected to relate to success in beat-based processing.

Individual Differences

Across the three experiments, individual differences appeared to influence how the audio-visual figure affected performance on grammaticality judgments. For children, the correlation between RA and RegAV remained significant after correction for multiple comparisons, while the correlation between RA and RegA fell short of significance, suggesting that the connection between RA and benefit of the visual cue may have been slightly stronger for children with higher RAs. The correlation of RA (and not CA) with performance after regular rhythmic primes was also observed in Fiveash et al. (2020). Links between language skills (e.g., grammar, phonological awareness, reading) and rhythm processing have been shown in the literature (Tierney and Kraus, 2013; Gordon et al., 2015a,b) and research is suggesting a link between speech and language impairments and rhythm processing (Ladányi et al., 2020; Fiveash et al., 2021). It is therefore possible that children with higher RAs were better able to use the visual cue to scaffold their beat perception and enhance its effect on subsequent speech processing.

The adult experiments showed that the effect of the visual cue differed depending on participants' scores on the sensory-motor and social sub-scales of the BMRQ (Mas-Herrero et al., 2013). The sensory-motor sub-scale included the questions: (1) *I don't like to dance, not even with music I like (reverse scored),* (2) *music often makes me dance,* (3) *I can't help humming or singing along to music that I like, and* (4) *when I hear a tune I like a lot I can't help tapping or moving to its beat.* In both adult experiments, participants who scored *lower* on the sensory-motor scale performed *better* after the RegAV rhythmic primes than the IrregA primes, whereas participants who scored *higher* on this scale performed *worse* after the RegAV primes than the IrregA primes. Previous research has suggested that participants use a visual cue more strongly when it is difficult to extract a beat from the auditory information (Su, 2014b). The authors interpret this finding within the *principle of inverse effectiveness* of multisensory integration, which suggests that as sensitivity to a unimodal stimulus decreases, the value of the multimodal cue increases (Meredith and Stein, 1986; Senkowski et al., 2011). In the current experiment the difficulty of the auditory rhythms was not manipulated. However, previous research has suggested that individual performance on a task can evoke the principle of inverse effectiveness (Caclin et al., 2011; Albouy et al., 2015). It is therefore possible that participants who were poorer at sensory-motor integration found it more difficult to extract a beat, and therefore relied more on the visual cue. Conversely, participants who had no trouble extracting the beat from the rhythms might have been more distracted by the bouncing figure, or focused on other body parts that were not necessarily aligned. Although with the current dataset it is not possible to investigate the level of attention or distraction during prime presentation, the current results suggest that individual differences should be monitored in future audio-visual experiments, and a measure of attention should be introduced.

In addition to the sensory-motor sub-scale influence, the social sub-scale of the BMRQ was a positive predictor of the difference between RegAV and IrregA performance in Experiment 3. This finding suggests that as participants scored higher on the social sub-scale, their performance was better after RegAV primes than IrregA primes, and as they scored lower on the social sub-scale, their performance was worse after RegAV primes. The social sub-scale included the questions: (1) *when I share music with someone I feel a special connection with that person,* (2) *music makes me bond with other people,* (3) *I like to sing or play an instrument with other people,* and (4) *at a concert I feel connected to the performers and the audience.* It is possible that participants with higher social scores were more engaged with the swaying figure on the screen, and therefore paid more attention to the visual cue, enhancing beat perception.

This suggestion is supported by research suggesting that in typically developing populations: (a) participants with higher empathy looked longer at social images than participants with lower empathy, who were quicker and more frequent to look away from social images (Hedger et al., 2018), (b) participants with fewer autistic traits became more precise over an experimental session for social, but not non-social stimuli compared to participants with higher autistic traits (Honisch et al., 2021), and (c) participant pairs with high empathic perspective taking were better at synchronizing together than participant pairs with low empathic perspective taking (Novembre et al., 2019). Taken together with the current results, it is possible that participants with higher social scores may have been more interested and paid more attention to the swaying visual cue, possible resulting in enhanced auditory-motor entrainment, resulting in a benefit of the visual cue. This interpretation is somewhat supported by the observation that the same pattern of results regarding the social scale was not observed for the bouncing figure in Experiment 2. It is indeed possible that the forward-facing swaying figure was more appealing and looked more "social" than the bouncing figure, which was facing to the left (to show more clearly the knee bend).

Limitations and Future Directions

There were some important differences in our study compared to previous studies showing enhanced beat-based processing with motor movement (e.g., Phillips-Silver and Trainor, 2007; Falk et al., 2017) or with a visual point-light figure (Su, 2014b). It might be that the motor movement element could be critical to enhance the auditory-motor link and its potential benefit for beat processing. We gave free instruction to our participants and told them that they were allowed to move along with the bouncing/swaying figure if they wanted to. However, we did not enforce the movement of participants, and other than observational data from the children, we did not record whether participants did move along with the rhythms (and if they did, whether they moved in time). Future research could more clearly activate this motor link and ask participants to directly move or tap in time with the visual figure. If a motor component is implemented, it would be important to monitor accuracy, as unsynchronized motor movements could be detrimental to beat-based processing. Further, a similar motor component should be introduced for the irregular rhythms to control for attention and task engagement; however, this implementation could be more difficult to define for irregular rhythms. The present experiments included a small training session so that participants were trained to focus on the synchronization of the point-light figure with the music, but a longer familiarization or training session (i.e., rhythmic tapping or rhythm workshop beforehand, as in Hidalgo et al., 2017) might have been necessary to enhance the effect of the visual cue.

Based on studies suggesting that moving visual cues are effective for synchronization (Silva and Castro, 2016; Torres et al., 2019), the inclusion of such a cue could particularly benefit beat perception and synchronization to rhythmic primes when a motor component is involved. This hypothesis is in line with auditory-motor studies showing enhanced cueing effects with additional motor synchronization (Falk and Dalla Bella, 2016; Falk et al., 2017). Therefore, we would predict that asking participants to synchronize with the regular primes might provide an enhanced rhythmic priming effect compared to purely auditory primes. However, it is also possible that adding an additional tapping task while also watching a visual moving figure and listening to the rhythms might become too complex if the full audio-visual percept cannot be integrated and/or the required additional tapping task taxes perception and cognitive resources. Future research could test these effects and investigate whether and how visual cues and the addition of movement could be used effectively to enhance synchronization within rhythmic priming paradigms. Individual differences would also be important to measure, as participants would most likely vary in their synchronization abilities, which could affect the quality of synchronization (e.g., Doelling and Poeppel, 2015; Assaneo et al., 2019).

Together with previous results, it appears that visual cues may be beneficial only under certain circumstances, in particular relating to attention and precision of the visual cue. Attending to the stimulus for 32 s may have been too long to maintain attention with the visual cue. In Su (2014b), attention was maintained (over short auditory sequences) by asking participants to additionally detect if one of the points on the point-light figure changed color. In future experiments investigating the influence of visual cues on rhythmic priming, it would be valuable to add an attentional check to measure attention to the cue and how it fluctuates over time. The stimuli in Su (2014b) were also carefully controlled. Recordings of natural movement were made and then manipulated to be more precise. Movement along the horizontal axis was removed, the feet markers were kept still even though they naturally moved in the original recording, and the least temporal deviation of one cycle of movement was used across all rhythms. In contrast, we had a musician bouncing or swaying in time with the rhythms for 32 s and did not manipulate this movement artificially. Therefore, our stimuli could be considered natural, but there were also likely to be small timing and movement deviations, which could have influenced the precise synchronization of the visual cue with the music. For example, movements of other body parts (e.g., arms, hands, and head) may not have been synchronized with the beat, and participants may have focused on these body parts rather than the aligned knee movements of the bouncing movement. For this reason, we changed our stimuli in Experiment 3 to a swaying figure with the aim to have more precise and clear visual cues to the beat, even though there was still free movement of the other body parts (e.g., arms, hands, and head). However, even with this manipulation there was still no advantage for the visual cue. The addition of a visual cue may therefore aid rhythm perception in particular for short rhythmic sequences and with very precise timing.

Finally, our findings revealed the potential influence of individual differences in whether the visual cue enhanced rhythmic entrainment or not. Future research could consider testing a larger sample of participants and including objective measures such as rhythm perception skills, as well as empathy and other social traits, for example. Note that the successful audio-visual experiments in Su (2014b) contained small sample sizes, with 14 participants in the same-different task and 11 participants (plus the author) in the synchronization task. It is possible that the included participants in Su's study were more strongly influenced than the general population by the visual cue (especially the author, who would have been very familiar with the visual cue). Future research investigating the influence of visual cues could therefore include manipulations of task, stimulus duration, and individual differences, as these appear to play important roles in the efficacy of the visual cue.

CONCLUSION

The current study showed that passively watching a visual point-light figure moving in time to regular rhythms removed the benefit of regular rhythmic primes on subsequent grammaticality processing. These results suggest that in the current experimental paradigm, the addition of a visual cue does not enhance beat perception and may detract from rhythmic entrainment. However, individual differences appeared to play an important role, as participants with low sensory-motor sensitivity benefited more from the visual cue, as did participants with high social sensitivity when the visual cue was facing forwards rather than sideways. The current study suggests that the task, the visual cue implementation, attention, and individual differences are all important elements as to whether visual cues aid beat perception and potentially benefit the rhythmic priming effect.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Comité de Protection des Personnes (CPP), France. For Experiment 1 (involving children), written informed consent to participate in this study was provided by the participants' legal guardian/next of kin. For Experiments 2 and 3 (involving adults), participants provided their written informed consent to participate in the study.

AUTHOR CONTRIBUTIONS

AF, L-HC, NB, and BT designed the study. AF and L-HC analyzed the data. AF wrote the first draft of the manuscript. AF, L-HC, and NB tested participants. AF, BB, L-HC, and BT contributed to the design of the point-light figures. BB provided the point-light figures. AF and BT completed and finalized the analyses and result presentation. BT and NB provided funding and resources. All authors edited the manuscript and interpreted the results.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.807987/full#supplementary-material

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Collective Rhythm as an Emergent Property During Human Social Coordination

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The literature on social interactions has shown that participants coordinate not only at the behavioral but also at the physiological and neural levels, and that this coordination gives a temporal structure to the individual and social dynamics. However, it has not been fully explored whether such temporal patterns emerge during interpersonal coordination beyond dyads, whether this phenomenon arises from complex cognitive mechanisms or from relatively simple rules of behavior, or which are the sociocultural processes that underlie this phenomenon. We review the evidence for the existence of group-level rhythmic patterns that result from social interactions and argue that the complexity of group dynamics can lead to temporal regularities that cannot be predicted from the individual periodicities: an emergent collective rhythm. Moreover, we use this interpretation of the literature to discuss how taking into account the sociocultural niche in which individuals develop can help explain the seemingly divergent results that have been reported on the social influences and consequences of interpersonal coordination. We make recommendations on further research to test these arguments and their relationship to the feeling of belonging and assimilation experienced during group dynamics.

Keywords: interpersonal coordination, collective rhythm, emergence, spontaneous mimicry, synchronization

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INTRODUCTION

The Mexican wave (hereinafter the wave) propagates in stadiums through the action of successive groups of fans who briefly stand up with their arms up (see Farkas et al., 2002). To anyone who has been part of it, it is evident that it arises from a small group of initiators, that no individual fan has control over its development, and that it expands spontaneously from the interaction between fans following a simple local rule such as "if the person next to you stands up, you stand up; if they sit down, you do so as well." In contrast, when seen from a distance, this collective behavior seems to have a life of its own, or a dynamic that does not easily correspond to the individual behaviors that start and sustain it throughout the stadium and whose development is not controlled by any agent or external factor. Coordinated activities like this are examples of *self-organizing emergent phenomena* that arise from and are sustained by the collective in non-intuitive ways (i.e., weak emergence: Bedau, 1997).

A dyadic interaction is a smaller scale and widely studied example of this type of self-organizing phenomenon. During social activities, participants not only spontaneously coordinate at the behavioral but also at the physiological and neural levels (Hoehl et al., 2021). This coordination organizes the biological rhythms of the individual (Feldman, 2012) and gives a temporal structure to the interpersonal dynamics. Importantly, in humans this phenomenon may signal affiliation and has been associated with prosocial behaviors (Gordon et al., 2020) and, indirectly, with the feeling of belonging and assimilation to the group that people experience when participating in collective activities such as rituals (Mogan et al., 2017). Although research on this topic has gradually shifted toward the study of interactions of more than two people and of more spontaneous, everyday activities, it is still not clear, for example, how the rhythmic patterns observed in group activities are related to the said sociocultural processes or if their characteristics are similar to those observed in dyads. Particularly, in the latter case, it remains to be addressed whether the temporal organization of a group activity is an example of self-organization emerging, as in the case of the wave, from the individual rhythms.

Examining whether a collective temporal pattern is an emergent phenomenon is important for our understanding of social complexity and cognition (see Boyer and Ramos-Fernandez, 2018). First, this knowledge could be used to explore the extent to which this temporal organization arises from complex cognitive mechanisms or from relatively simple rules of behavior, such as those required for the wave. Second, the study of emergent collective rhythms could inform us about the cognitive capacities supporting the perception of group movement (e.g., Cracco et al., 2021) or those associated with rhythm perception and production (Ravignani et al., 2014). Finally, it could be used to complement our understanding of sociocultural practices such as collective effervescence (Xygalatas et al., 2011) or musical improvisation (Walton et al., 2015).

In this contribution, we put forward the hypothesis that collective rhythms emerge during naturalistic interactions, as the basis for further research in this area. We review some of the evidence that supports this hypothesis and the relationship of macroscopic phenomena with the social processes that have been associated with them. We begin by proposing a definition of collective rhythm, and then review two mechanisms that have been frequently used to explain patterns, both in time and form, of interpersonal coordination: behavior matching and interactional synchrony (Bernieri and Rosenthal, 1991). We then propose a framework on how these mechanisms can be used as minimal explanations of the temporal organization of social interactions at the individual and group levels, and how taking their social impact into account can help explain seemingly divergent results on their functional significance in the literature. The final section integrates the evidence to explore whether coordinated activities could lead to the emergence of a collective rhythm, its relationship to the group feeling of belonging and connection, and if such phenomena could be integrated into the construction of the human niche.

Definition of Collective Rhythm

The organization of behavioral events and its development over time build up the temporal structure of behavior (e.g., Ravignani et al., 2014). In a single individual, complex behaviors are temporally structured by layers of multimodal signals (Pouw and Dixon, 2020) nested on different time scales (Abney et al., 2021). For example, several occurrences of body movements and utterance activity produced at short scales (e.g., typing) can be grouped into larger time scales, in turn delimited by moments of no activity (e.g., writing a chapter of a manuscript in short bursts). Likewise, in even larger time scales, such ensembles of behavioral activity can be arranged in clusters depending on the constraints and contingencies of the various stages of the task at hand (e.g., planning, writing, evaluation). This type of temporal pattern (i.e., the duration and timing of events) of the nested organization of any series of behavioral or physiological activity builds the rhythm of the individual (Ravignani and Norton, 2017).

When several people are involved in a joint behavioral event (chorus behavior, sensu Ravignani et al., 2014), the temporal pattern of each individual reflects the dynamics of their interaction (**Figure 1A**), in the sense that participants reciprocally adjust their behaviors to the actions and reactions of others and the environment in which they interact. At one end, a group in which each individual behaves independently of the others (for example, tossing a coin and taking a step to the left or the right depending on whether it is heads or tails), will have disconnected temporal patterns. At the opposite end, a group in which its participants influence and are influenced by other participants' behavior will show a varying degree of temporal organization depending on the individual and collective constraints and contingencies of the task in question. For example, the temporal structure will vary whether people sing in unison (e.g., synchrony), coordinate into subgroups to build a Lego structure (e.g., complementary) or enter a roundabout (e.g., alternating).

In longer timescales, these individual temporal patterns and the joint dynamics of the interaction can change over time (Wiltshire et al., 2018). Some common examples of this evolution are the temporal patterns of body movement during music improvisation, the steps of pedestrians passing over a footbridge and the swing of metronomes placed on a moving surface, which start out as decoupled patterns (i.e., independent) and eventually fall into coordinated behaviors (e.g., simultaneous or alternating) because the medium in which they interact (i.e., music, shaking surface) couples them weakly.

The timing and duration of behavior events recovered from all participants at the same time (**Figure 1A**) can be used to describe the rhythm of a given group. However, as mentioned above, it is still unknown to what extent and under which circumstances these collective rhythms are emergent self-organizing temporal patterns. Then, in order to facilitate its study, we define an *emergent collective rhythm* (**Figure 1B**) as the temporal patterns of behavior arising in groups that cannot be predicted from the individual periodicities alone. These patterns can be thought of as a group-level property, in this case, a rhythm "with a life of its own," analogous to the wave observed in crowded stadiums. Moreover, similar to the rhythm in music, this group-level phenomenon could be a temporal pattern with which individuals could coordinate. However, in contrast to a prespecified rhythm provided by a musical sheet (i.e., an external controlling component), the collective rhythm would both influence and

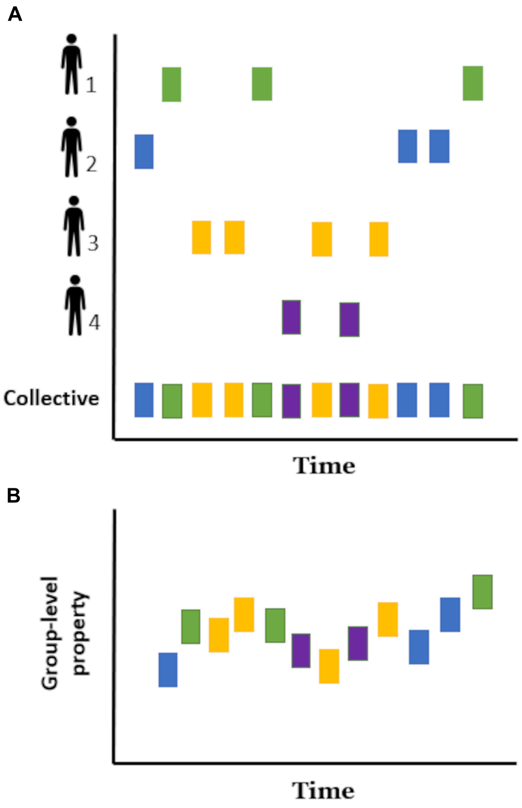

FIGURE 1 | Schematic representation of temporal rhythmic patterns in a group of four individuals. The onset time of a given behavioral event (e.g., an utterance) is represented as a rectangle with each color corresponding to a different individual. **(A)** Temporal patterns of behavior recovered from each of the four individuals (individual temporal patterns) and from all participants (collective temporal pattern). **(B)** Emergent collective rhythm: a collective temporal pattern that cannot be predicted from the individual periodicities alone. In this case, the vertical axis represents a new group-level property.

be influenced by the individual rhythms and contingencies of the interaction. This is not to say that musicians do not take part in instances of emergent collective rhythm, given that music improvisation is a great example of this group phenomenon.

Different emergent forms of social coordination have been reported (spontaneous coordination: Knoblich et al., 2011; synergy: Fusaroli et al., 2014; self-similarity: Abney et al., 2021), but the study of this emergence in the context of rhythmic patterns has been carried out mainly in dyads and on short timescales. However, this approach disregards that, over time, the specific arrangement of interactions between participants and between them and the environment can produce dynamics that are not easily predictable (Page, 2015). Moreover, it overlooks that once formed, group-level phenomena can constrain the evolution of the individual components and produce even more complex dynamics (i.e., downward causation: Flack, 2017). In both cases, this path dependency would mean that the outcome of a coordination dynamic, either in terms of the resulting temporal pattern or its social consequences, is contingent on what happens during its evolution. And in such circumstances, focusing only on certain moments of the interaction and ignoring its change over time may lead to incorrect inferences. Therefore, the study of emergent collective rhythms also needs to consider these dynamics over time as well as the possibility of downward causation from the macroscopic to the microscopic level.

MECHANISMS

In this section we review two mechanisms that have been frequently used to explain coordination dynamics: behavior matching and interactional synchrony. We chose these mechanisms as the simplest explanation of how behavior can spontaneously be organized: people unintentionally mimic (Lakin and Chartrand, 2003) and synchronize (Knoblich et al., 2011) their behavior with others. Furthermore, we chose these mechanisms because they have been studied in species other than humans. This evolutionary perspective seeks to complement previous accounts of interpersonal coordination based on processes observed solely in contemporary humans (e.g., behavioral alignment: Rasenberg et al., 2020, interpersonal synergies: Fusaroli and Tylén, 2016, coordination: Clayton et al., 2020), and to encourage its use to compare different systems of animal behavior.

Behavior Matching

People involuntarily imitate the movements and facial expressions of others. Although the terminology used to explain this phenomenon depends on the domain (Genschow et al., 2017), here, the concept of *behavior matching* encompasses both the study of spontaneous mimicry and automatic imitation.

When coordinating with others, we observe a tendency to spontaneously adopt the behaviors of interaction partners (Lakin et al., 2003), even if it affects the efficiency of the observer's own movements (Forbes and Hamilton, 2017). Importantly, this automatic tendency to imitate is fundamental in contexts in which participants need to predict others' movements (Sacheli et al., 2015; Era et al., 2020), suggesting that automatic imitation is associated with action prediction during interpersonal motor coordination.

Behavior matching can occur from fractions of a second (e.g., finger mimicry) to several seconds (e.g., yawning) after the stimulus (Prochazkova and Kret, 2017; Arnold and Winkielman, 2019). And in scenarios in which individuals automatically imitate the actions of multiple agents (Cracco et al., 2015), the response time decreases asymptotically when the observed movements were congruent and increase linearly on incongruent ones (Cracco and Brass, 2018).

Spontaneous mimicry is based on motor resonance, where the action of observing others activates neurons that represent that same action in the observer's motor system (cf. Uithol et al., 2011, on controversies in the interpretation of motor resonance). This phenomenon is thought to allow for a quick communication with other members of the group about important aspects of the physical and the social environment (e.g., physiological internal states like arousal due to food availability or fear due to predator presence). For instance, in different species of mammals, mimicry has been found to be associated with socially relevant facial displays, such as the play face (Palagi et al., 2020), which is assumed to communicate a playful mood (Palagi et al., 2019) even when phylogenetically distant species play together (e.g., Maglieri et al., 2020). Motor resonance is also communicative because it affects how individuals perceive their surroundings. For example, in a series of experiments, Fini et al. (2017) showed that extra-personal space representation is a function not only of the individual's motor potential but also of the bodies, motion, and intentions of other individuals. In addition, it has also been proposed that spontaneous mimicry underlies emotional contagion, whereby the perception of another's emotional state automatically activates the same neural response (including the mirror neuron system) of the affective state in the observer, along with corresponding somatic and autonomic responses (Xavier et al., 2016; Palagi and Scopa, 2017; Prochazkova and Kret, 2017).

By creating similarity between participants and by providing a basis for inferring other's emotions, both behavior matching and emotional contagion are linked to empathy, rapport, and prosocial behavior (see Lakin et al., 2003). These prosocial consequences facilitate interactions and coordination of common goals, for example, by conveying the readiness for coordinated action (e.g., playful interactions: Palagi and Scopa, 2017; music and dance: Phillips-Silver and Keller, 2012), by smoothing the interaction and making it low-maintenance (see Lakin, 2013), or by communicating the social role of the interactants (e.g., dominance in primates: Palagi et al., 2020).

Despite the potential role of spontaneous mimicry in social interactions, its ontogeny has been little explored. We know, for example, that mimicry of facial expressions is present in neonates (Palagi and Scopa, 2017, but see Oostenbroek et al., 2016), and that in infants, it occurs in response to multimodal, not unimodal information (visual or auditory separately, Isomura and Nakano, 2016), and to happy and fearful faces as opposed to angry faces (Kaiser et al., 2017). Additionally, the tendency to mimic is positively related to the amount of facial imitation received from the caretaker (Klerk et al., 2018) and modulated by the quality of early attachment relationships (Vacaru et al., 2020). Later in life, individuals mimic more smiling faces than angry, fearful or sad faces (Sachisthal et al., 2016), and are more aroused at pleasant, but not unpleasant facial expressions (Fujimura et al., 2010). The mimicry response can be further influenced by the *a priori* levels of empathy of the mimicker (Rymarczyk et al., 2016), and of liking for the person being mimicked (Stel et al., 2010).

Overall, the individual mimicry response has been shown to be a stable individual trait (Hess et al., 2016) reduced in the absence of social utility (Beffara et al., 2012) and modulated by social cues about the type of task performed (Arnold and Winkielman, 2019; Era et al., 2020) or group membership (Sacheli et al., 2015; van Schaik and Hunnius, 2016; de Klerk et al., 2019) even in different mammalian species (Palagi et al., 2020). Furthermore, studies on power dynamics in humans have shown that spontaneous mimicry not only follows simple direct-matching rules (e.g., smile to a smile) but that social cues like hierarchy can lead to the counter-mimicry or opposite matching (Arnold and Winkielman, 2019; Palagi et al., 2020), such as when high-power perceivers smile in response to angry expressions of other high-power targets (Carr et al., 2014).

In sum, spontaneous mimicry of others' behavior is an important component of interpersonal coordination that facilitates the interaction and promotes affiliation.

Interactional Synchrony

During social interactions, we not only observe an automatic imitation of perceived behaviors, but also that individuals are able to anticipate other's behaviors and align the timing of their movements accordingly. Integrating the evidence on this ability is complicated because the terminology used to refer to it changes depending on the discipline. We chose the concept of interactional synchrony (Bernieri and Rosenthal, 1991) to encompass this variability because it includes two broad subfields: the study of *entrainment* and of *synchronization*. Although both deal with the temporal coordination of two or more events (Bittman, 2021), the first one focus on the ability of an individual's endogenous rhythms to entrain to time cues at a variety of phase angles, while the second with the ability of an individual's locomotor rhythms to align in phase to a given time cue. Therefore, we use the term entrainment only to refer to endogenous rhythms and synchronization everywhere else.

In the two sections below, we focus separately on endogenous rhythm and its entrainment and on spontaneous motor tempo (SMT) and its synchronization. We review studies that complement previous accounts of the production and perception of rhythm in music and speech (Ravignani et al., 2017), and that emphasize the potential role of the plasticity and development of the individual's internal rhythms in our ability to recognize and synchronize with the rhythms of others. In particular, we highlight that in both cases the flexibility and propensity to which individuals coordinate with others is modulated by the experience they have during development (e.g., parental coordination strategies, musical training) and the emotional context of the interaction.

Endogenous Rhythms

Endogenous rhythms (Kriegsfeld and Nelson, 2009) are ubiquitous in nature and are assumed to be the organism's adaptation to the highly predictable and cyclic environment that results from physical forces (e.g., the light-dark cycle - LD-, the seasons). They are regulated by the organism's biological clock and have cycles in the millisecond-to-year range. Importantly, endogenous rhythms are self-sustained and can synchronize with rhythmic signals, i.e., they will continue to cycle in the absence of any time cue but will actively entrain in the presence of one. Entraining favors the alignment of behavioral and physiological rhythms to those of the environment: for example, instead of responding to the immediate food availability, organisms keep track of time internally, which allows them to anticipate changes in such resources throughout the day or year and to respond accordingly, even when temporal cues are unavailable (e.g., in caves) or misleading (e.g., light exposure in urbanized environments) (Helm et al., 2017).

In social species, activities to be performed together with conspecifics (e.g., foraging, mating) also form part of the temporal layout of the environment, i.e., the arrangement of biotic and abiotic rhythms whose different periodicities are overlapping in the environment and with which organisms can align. Failure to keep up with these activities could make an individual more susceptible to predation or ostracism. Accordingly, social stimuli have been shown to entrain endogenous rhythms (Mistlberger and Skene, 2004; Favreau et al., 2009; Bloch et al., 2013) both in species with limited access to the main environmental time cue, i.e., the LD cycle, or those living on natural LD cycles. For example, the circadian synchronization of marmosets placed in temporal isolation (i.e., constant light condition) is favored by the activity profile (Melo et al., 2013) or vocalizations (da Silva et al., 2014, but see Erkert et al., 1986) of conspecifics, or acoustic and olfactive contact between reproductive pairs (Bessa et al., 2018). In humans, the evidence suggests that social signals are weaker than light cues, but both jointly influence the circadian response (i.e., rhythms with cycles of approximately 24-h) (Davidson and Menaker, 2003; Mistlberger and Skene, 2004).

Evidence for the role of endogenous rhythms in social coordination is found in studies addressing the mother-infant attunement, essential to the offspring's survival (Harrist and Waugh, 2002). In these studies, synchrony facilitates the coordination of hormonal, physiological, and behavioral cues into an affiliative bond that facilitates individuals' physiological regulation during development. For example, we know that fetal rhythms engage with the LD cycle indirectly through maternal signals (e.g., body temperature), that the mother's heart rate or walking pace facilitate the infant's physiological regulation (Bobin-Bègue, 2019), and that during face-to-face interaction, vocal and affect exchanges increase the degree of physiological linkage (Feldman, 2012). Moreover, such physiological dynamics have been associated with emotion regulation and empathy levels later in life (Lee et al., 2017; Levy et al., 2019; Levy and Feldman, 2019).

Overall, this literature shows that individuals in many animal species, including humans, are capable of processing rhythms and synchronizing with the immediate social environment even before birth. By underpinning the child's social and emotional growth, this ability is in turn crucial in shaping the adult's ability to coordinate and relate to others.

Spontaneous Motor Tempo

Throughout life, we regularly carry out rhythmic locomotor activities (e.g., infant's spontaneous sucking, walking) that show a self-sustained repetition rate and the ability to synchronize with rhythmic signals, i.e., we all have a preferred pace to perform them, but we can synchronize them with an external time cue with a different pace (e.g., clapping to the beat of a song). This preferred, "internal," "natural" tempo or SMT is speculated to reflect the intrinsic tempo of a spinal central pattern generator (MacDougall and Moore, 2005). It has been studied mostly by using a tapping task where participants are asked to tap their hands on a table at a comfortable rate (McAuley, 2010), showing that SMT is an individual trait that develops throughout ontogeny, becoming slower and more stable in adulthood (McAuley, 2010; Bobin-Bègue, 2019; Monier and Droit-Volet, 2019). Even when different movements within an individual have different tempi (e.g., Qi et al., 2019), there is a preference for 500 ms periods, either during everyday locomotor activity or activities performed in laboratory conditions (MacDougall and Moore, 2005).

Humans and a few other species (Wilson and Cook, 2016) can synchronize these motor tempi with external temporal signals. Particularly, humans are able to adapt to tempi that are different from their SMT, either deliberately as in tapping tasks (Repp and Su, 2013) or spontaneously, as when neonates modify the tempo of their sucking (Bobin-Bègue et al., 2006) or stepping (Provasi et al., 2014) according to a rhythmic stimulus, or when music engages infant's movements (Zentner and Eerola, 2010) or the walking pace of adults (Buhmann et al., 2016). Studies using a variation of the tapping task show that flexibility in synchronization to different tempi develops with the maturation of the neuromuscular system during the first years of life, that it reaches its adult form at about 8–10 years old (Provasi and Bobin-Bègue, 2003; Rocha and Mareschal, 2016), and that its accuracy can be improved by extensive training. Indeed, musicians synchronize more flexibly across tempi than non-musicians (Scheurich et al., 2018) but even after this rigorous training, the spontaneous rates at which they perform naturally (i.e., SMT) remain stable (Zamm et al., 2018). Simultaneously, this flexible response to new tempi and its accuracy are also influenced by the individual's internal tempo. During synchronization tasks, musicians with a more stable tempo are more synchronous across different tempi (Scheurich et al., 2018), while synchronization accuracy increases when the external cue is close to the individual's SMT (Loehr and Palmer, 2011).

Although the above characteristics make the internal motor tempo a potential key coordinating mechanism for social interactions (Jungers et al., 2002), there is little research on the role of its flexibility within a social context. On the one hand, we know that the individual's tempo influences the accuracy in the timing with others. For example, a similar SMT between participants when walking side by side facilitates synchronization to the other's movements (Repp and Su, 2013). Likewise, musicians with matching spontaneous rates of solo performance show greater synchrony than mismatched partners (Jungers et al., 2002; Loehr and Palmer, 2011; Palmer et al., 2019). On the other hand, the social environment may influence the accuracy of such synchronization. For instance, although children as young as 2.5 years are unable to synchronize with acoustic pulses, those that drum together with an adult can do so with high accuracy, as opposed to when drumming along an audio-visual or an acoustic stimulus (Kirschner and Tomasello, 2009). In addition, children's previous everyday experiences and the musical practices within their culture could also influence whether a child will spontaneously synchronize with the experimenter and the accuracy of this task (Kirschner and Ilari, 2013). Moreover, the previous experience of the infant's own body movement (i.e., being moved up and down to a beat) plays an important role in their rhythm perception and listening preferences (Phillips-Silver and Trainor, 2005).

We also know that its ability to adapt allows the internal tempo to modulate and be modulated by others' tempi from very early in development. For example, infants move their limbs in coordination with the speech behavior of adults (Condon and Sander, 1974) while adults change their speech rate according to infants' linguistic competence (Narayan and McDermott, 2016). Finally, we know that despite being a relatively stable trait, the individual's internal tempo may vary depending on the emotional context of the interaction, and that this will affect its ability to synchronize with a beat (Monier and Droit-Volet, 2016).

Summing up, during interpersonal coordination, the rhythms (i.e., endogenous, SMT) of different individuals interact in a shared temporal structure. Given that these rhythms can be synchronized with temporal cues with great flexibility and accuracy, they are potentially key to such integration, affecting and being affected by social exchanges. They represent stable individual differences in the pace of periodic movements, and, at the same time, encompass the fluctuations that individuals experience due to, for example, the emotional context of an interaction. During activities that follow tempi with a high degree of consistency (e.g., music), the synchronization is more accurate when the task's tempo is closer to the tempo of the participants. Whereas during activities that are not constrained by a prescribed tempo, that is, those in which no agent controls the development of the dynamic (e.g., face-to-face interaction), a certain degree of flexibility may facilitate the mutual modulation.

BODILY STATES AND THE TEMPORAL PATTERN OF BEHAVIOR

An emergent group-level phenomenon depends strongly on the specific way in which its components combine and interact (Page, 2015). Therefore, in this section we emphasize how spontaneous mimicry and synchrony contribute to the integration of temporal patterns during social interactions at the individual (i.e., bodily state) and group level (i.e., collective temporal pattern), and how this could lead to an emergent collective rhythm. The assumptions underlying this argument are presented in a simple causal model (Rohrer, 2018) below.

According to the evidence presented so far (see section "Mechanisms"), behavior matching and interactional synchrony are key in organizing the temporal structure of an interaction. On the one hand, either as a sequence of discrete events between individuals or as the onset of coordinated behaviors between them (e.g., Casetta et al., 2021), behavior matching (**Figure 2A**) marks the onset of a given behavior and, thus, builds its temporal pattern (see **Figure 1**). On the other, given that the individual rhythms (i.e., endogenous, SMT) can be synchronized with temporal cues with great flexibility (i.e., varying phases) and accuracy, interactional synchronization (**Figure 2B**) could organize the temporal patterns of different participants by reducing the rhythmic diversity between them to a single rhythm, to alternate rhythms or by producing rhythms coupled to varying degrees. Contingencies and constraints at this individual level will create variability in the outcome observed for each mechanism and thus influence the social dynamics. For instance, *a priori* levels of liking to the other participants will change an individual's tendency to mimic others (Stel et al., 2010) while an individual's internal tempo will affect the accuracy with which they synchronize to others' temporal cues (Loehr and Palmer, 2011).

In practice, behavioral matching and synchronization are intertwined and often used interchangeably. One example of their tangled expression has been observed in studies on our ability to process temporal information. According to this research, although our internal clock allows us to accurately estimate time, its representation can be distorted by the physiological activation of emotional arousal (see Droit-Volet, 2019**:** 112). At the same time, spontaneous mimicry of emotional facial expressions activates such physiological arousal, thus potentially influencing the perception of time. Accordingly, the perception of another's emotional face distorts the accuracy of the estimate of the duration of the presented stimuli, but there is no temporal distortion if facial mimicry is inhibited by asking the participants to hold a pen between their lips (Effron et al., 2006). These results suggest that during an interaction both phenomena might entail a labile response (**Figure 3A**: bodily state) that appears to be integrated in the organism, particularly in situations with affective content (e.g., parent-infant interaction). In other words, contingencies at the interaction level, like those related to its affective context, may promote variability in this labile response. For instance, paying attention to an audiovisual stimulus (e.g., listening to the same story: Pérez et al., 2021) leads to spontaneous synchronization (**Figure 3**: spontaneous coordination) between participants, but the extent of this coordination depends on the emotional content of such stimulus and the existent social relationships between the individuals (Bizzego et al., 2020). Another example of how these interactions promote non-intuitive or easily predictable outcomes is the study of Gleibs et al. (2016). This study shows that the effect of group membership on automatic imitation between participants depends on the expected goal of the interaction. More precisely, when the goal is to compete, participants imitate to the same extent an ingroup than an outgroup target. Conversely, for cooperation, group membership is important: participants imitate more an ingroup than an outgroup target.

Likewise, the cultural niche in which individuals interact and develop produces constraints and contingencies that affect the development of a given social interaction. We know that organisms not only adapt to the environment, but that by transforming it, they modify the selection pressures that act on themselves through the process of niche construction (Laland and O'Brien, 2011). Humans modify their environment mainly through cultural processes, which impacts developmental processes and the traits that are considered as adaptive within a given population at a given point in time. Individuals will differ in their propensity to coordinate bodily states with others or the activities that trigger such coordination because of growing up in different culturally constructed environments (**Figure 3A**: social environment), or due to differences in the way in which cooperation, or empathy are encoded within the sociocultural context, different norms or cultural preferences, or differences in the social valence associated with the activities that are related to prosocial or to antisocial effects. For instance, even though children synchronize their drumming with higher

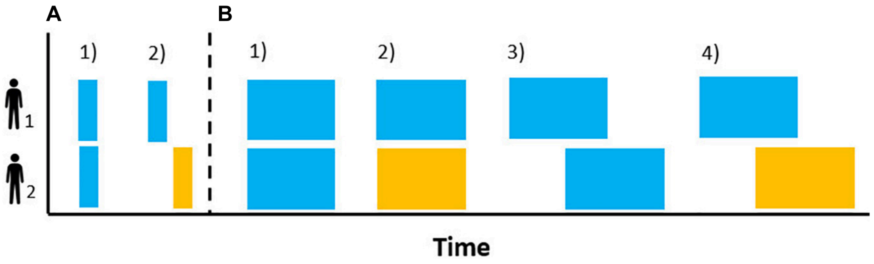

FIGURE 2 | Schematic representation of discrete **(A)** and continuous **(B)** patterns of observed behaviors at the level of the interaction. Behavior matching of the same behavior without lag [**(A1)** person matching the smile of the other interactant] or with lag [**(A2)** listening to another yawn activating the listener's yawn]. Synchrony of the same behavior [**(B1)** clapping together] and different behavior [**(B2)** the infant's arm movements matching in time and intensity the mother's voice], both matching in time. Synchrony of the same [**(B3)** the pitch of one person matching the pitch contour of the previous intervention] and different [**(B4)** the rhythm of someone's nod matching with a slight offset the speech rhythm of another] behaviors with lagged timing.

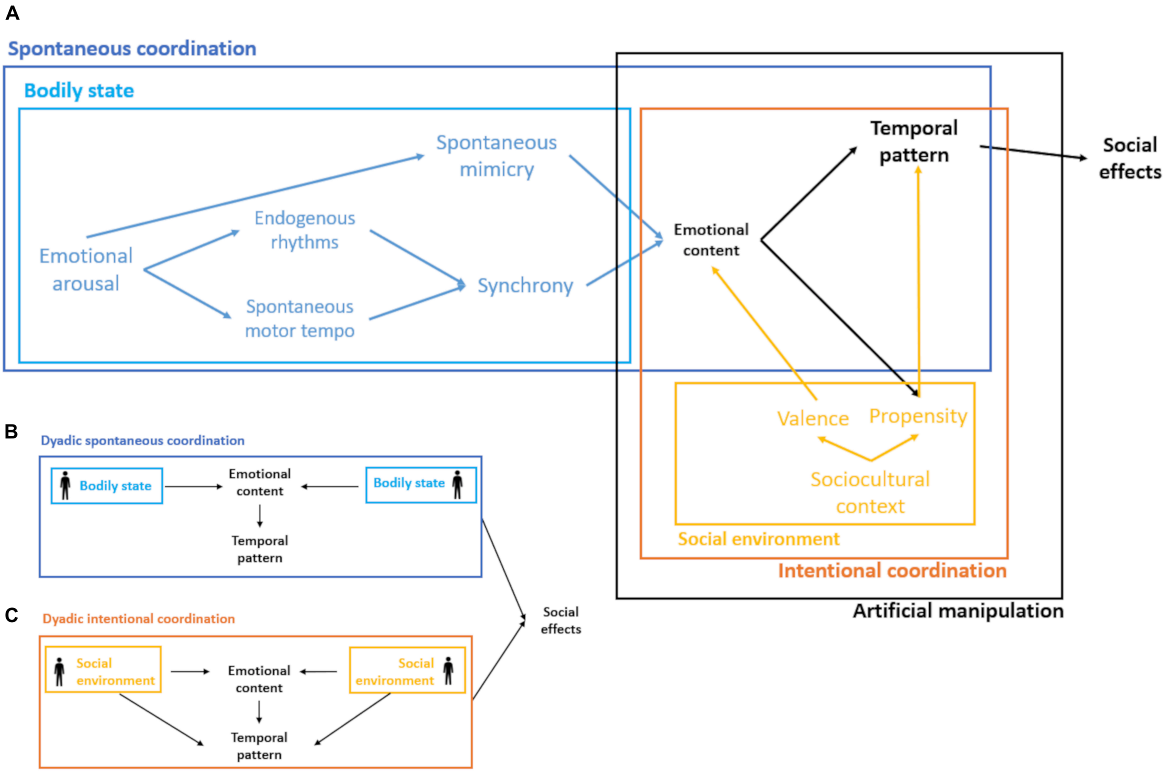

FIGURE 3 | Schematic representation of interpersonal coordination and its social effects. **(A)** Bodily state: depicts the intra-individual variation due to changes in emotional arousal affecting the individual's propensity to mimic and synchronize; the latter mediated by the individual's rhythms (e.g., endogenous rhythms and spontaneous motor tempo). Spontaneous coordination arises, at least in part, from the accommodation of bodily states between interactants. Social environment refers to the context in which individuals develop, which influences, for example, their propensity to participate in coordinated activities or the social valence that define prosocial or antisocial behavior. Intentional coordination considers the influences of the social environment at the interaction level. Artificial manipulation includes instances in which intentional coordination is artificially manipulated. **(B)** Dyadic spontaneous coordination: the exchange of bodily states between interactants influences, at the interaction level, the dynamics of emotional content and the temporal pattern of behavior. **(C)** Dyadic intentional coordination: like panel **(B)** but with an additional influence of the social environment on the temporal pattern, for example, when the goal of a task (e.g., to compete or cooperate) and the participants' social structure constraints the set of observed behaviors during the interaction.

accuracy to that of a human partner than to an external acoustic stimulus (Kirschner and Tomasello, 2009), Brazilian children were reported to do so more spontaneously and with greater accuracy than German children (Kirschner and Ilari, 2013). Importantly, the authors found that these differences were partially explained by differences in children's active musical practice at home. These results may suggest that the culture's practice (i.e., the constructed niche) in which the individual develops modulates the tendency to coordinate with others but not necessarily affects the individual ability *per se*. In other words, given a similar cultural environment, both groups of children would not differ on average in the accuracy and propensity to coordinate with others. Thus, the influence of the social environment on interpersonal coordination (**Figures 3A,C**: intentional coordination), could be incorporated not directly through mimicry and synchrony, but through the emotional content and the type of temporal pattern unfolded at the interaction level due to cultural encodings. Although there are no systematic reviews of cross-cultural differences in this regard, both spontaneous mimicry and synchronization have been reported to be sensitive to sociocultural cues, such as social status (Boukarras et al., 2021), group membership (Sacheli et al., 2015; Palagi et al., 2020) or the degree of competition of the task (Spapé et al., 2013; Era et al., 2020).

All these constraints and contingencies will feed back and influence whether during an interaction one participant adapts to the changes of others (unidirectional: Demos et al., 2017) or whether participants adapt and respond to one another (bidirectional: Lorenz et al., 2014). Nevertheless, while the former requires one participant to do all the adapting, the latter gives the participants an opportunity to modulate each other's bodily states and opens up the possibility of a new, more stable form of interaction that is different from the initial behavior of each individual, i.e., an emergent organization (Shockley et al., 2009). An example of such emergence would be the affective responses of patients and therapists, which stabilize around a homeostatic balance (Koole and Tschacher, 2016). Although uni- and bi-directional types of interactions would help structure the collective rhythm, an emergent collective rhythm, as defined previously, can only arise from the mutual modulation observed during bi-directional coupling.

The Social Effects of Interpersonal Coordination

Considering that the coordination of bodily states may facilitate or attenuate a shared experience and common timing with our conspecifics and may foster physiological homeostasis and emotional regulation within the individual, it is not surprising that it has been linked to different social effects (**Figure 3**), such as wellbeing, social cohesion and the feeling of connection (Wheatley et al., 2012; Prochazkova and Kret, 2017). Even though other mechanisms (e.g., shared purpose or intentions) may explain those social effects, our approach emphasizes that the spontaneous coordination of bodily states may increase the probability of experiencing them.

These positive effects have also been reported beyond dyads (von Zimmermann and Richardson, 2016; Jackson et al., 2018), particularly, physiological synchronization has been associated with group cohesion during, for example, teamwork or musical performance (Palumbo et al., 2016), and growing evidence in other social contexts suggests that this relationship is complex and non-linear (Palumbo et al., 2016; Wallot et al., 2016; Wood et al., 2018; Wiltshire et al., 2019; Mayo and Gordon, 2020; Dumas and Fairhurst, 2021; Hoehl et al., 2021). To the best of our knowledge, the only evidence of the prosocial consequences of mimicry at a group level is in studies of emotional contagion (e.g., Barsade, 2002), but they do not specifically tackle spontaneous mimicry. In non-human primates, some studies have related spontaneous facial mimicry to the development and maintenance of social bonds through social play (Palagi et al., 2019; Anderson and Kinnally, 2021). Likewise, whether the social consequences of behavioral mimicry also exhibit complex patterns at the group level has been little explored (see Hess, 2019).

Remarkably, the social effects that result from interpersonal coordination can also be accessed under artificial conditions (**Figure 3A**: artificial manipulation). In other words, once the inner workings of the coordination phenomenon are understood, humans can exert control over their own and others' experiences of connection (Wheatley et al., 2012). Specifically, creating an artificial experience by setting off a coordinated activity has been shown to promote prosocial effects. For example, participants asked to move their bodies in synchrony show physiological linkage and report increased rapport (Lakin et al., 2003; Wheatley et al., 2012), even within an immersive virtual reality environment (Tarr et al., 2018). Likewise, manipulating the emotional content of an interaction can create affiliation and rapport between participants. Individuals primed to the concept of affiliation before a word scramble task have been shown to increase mimicry responses, particularly in contexts where the goal is to create rapport with others (Lakin and Chartrand, 2003). However, unlike synchrony, mimicry was found not to increase rapport or trust in virtual scenarios (Hale and Hamilton, 2016).

This artificial manipulation has also been shown to promote antisocial effects; for example, aggression, destructive obedience and reduced creativity and dissent have been observed after asking participants to perform synchronized activities such as walking or singing (Gelfand et al., 2020, but see Mogan et al., 2019). This artificial manipulation can even lead to a complete disruption of social effects, like when synchronization is inhibited by asking participants to follow a beat asynchronously (Hove and Risen, 2009). Nonetheless, while disrupting facial mimicry (e.g., holding a pencil in the mouth: Palagi et al., 2020; administration of hormones: Kraaijenvanger et al., 2017) hinders recognition of other's facial and body expressions, it is not clear to what extent this affects affective bonds, empathy or the sense of belonging among interactants during naturalistic group activities.

In sum, the clearest picture we have of the social effects of interpersonal coordination through mimicry and synchrony is biased toward prosocial phenomena and dyadic interactions. Distinguishing the emotional and sociocultural constraints and contingencies at the individual level (e.g., levels of empathy, internal tempo) from those at the level of the interaction (e.g., emotional content, goal, complexity of the task) and at the social level (e.g., social niche) can help to deepen our understanding of this complex relationship and its characteristics in both natural and artificial settings, for example, by shedding light on whether the cultural encoding in the participants is accountable for the antisocial effects observed during artificial manipulations, or whether individual differences in internal tempo can impact the intensity of the social effects reported by the participants of an interaction.

DISCUSSION

Collective Rhythm

Remarkable examples of the emergence of a collective rhythm are the activity cycles of ants, the shimmering waves propagated across the colony surface of giant bees, or the "Mexican wave" behavior performed by crowds in stadiums (Couzin, 2018). As a group level phenomenon, this rhythmicity could enhance the chances of survival and reproduction, such as in the giant honeybees that have been shown to use shimmering as a colony defense against hornets (Kastberger et al., 2008). As mentioned before, the capacity to influence and be influenced by others' bodily states in non-intuitive, complex ways suggests that there is a possibility that during group dynamics a collective rhythm emerges from the temporal organization of behavior at the individual level.

Taking the evidence presented so far, in the sections below we explore some of the properties that could be associated with an emergent collective rhythm, and how this group-level phenomenon could be related to a collective feeling of wellbeing and connection. Additionally, we argue that this phenomenon could be artificially manipulated according to the sociocultural context, in a similar way as it has been reported for small-scale interactions.

The Properties of an Emergent Collective Rhythm

In general, very little has been explored about an emergent collective rhythm, but two approaches have given insights on its properties. On the one hand, the structural organization of some behaviors shows similar clustering across a wide range of time scales (e.g., conversation: Abney et al., 2014). This hierarchical clustering is observed commonly in language, where syllables are nested in words and words in sentences, sentences in interventions, and so on. Changes in speaking rate, for example, can affect how these events are clustered over time (Ramírez-Aristizabal et al., 2018). This has also been observed in, for example, the temporal pattern from seconds to hours of the locomotor activity of quails (Guzmán et al., 2017). Additionally, the pattern of resting periods of mice and healthy humans has been observed to be more nested than that of mice without a circadian clock gene or humans suffering from major depressive disorders (Nakamura et al., 2008). Likewise, the pattern of acoustic events of interactions between either speakers, musicians or killer whales is more nested than their individual rhythmic patterns (Kello et al., 2017). If we consider that the nested organization of spontaneous behaviors is found in several species, and that it is greater in healthy individuals and in contexts in which several individuals are involved, it is reasonable to expect that a collective rhythm emerging from group activities will exhibit a nested clustering of behavioral onsets at different time scales. However, more research is needed on this global phenomenon in group activities.

On the other hand, some behaviors are characterized by a lower variability than that observed in each participant's movements, i.e., dimensional compression (Riley et al., 2011; Fusaroli et al., 2014; Nowak et al., 2017). This reduced dimensionality of individuals' movements or synergies has been observed in the temporal pattern of speech/pause dynamics during conversation (Fusaroli and Tylén, 2016) or in the walking direction and the common speed that emerge in pedestrians (Kiefer et al., 2017). In the case of a collective rhythm, this reduced variability could be interpreted as a more predictable rhythmicity, and its presence could signal affiliation (e.g., Fawcett and Tunçgenç, 2017) or could facilitate the interpersonal coordination of observers, as a steady pulse does in music. In any case, more research is needed on these topics.

Research on collective rhythm would benefit if instead of equating social coordination to the concept of synchronization and considering dynamics as an endless alignment between systems, more complex and multilayered dynamics were included (Fusaroli et al., 2014; Wood et al., 2018; Clayton et al., 2020). Social coordination may include, for instance, compensatory exchanges (e.g., dancing partners movements) where the behavioral repertoire of an individual limits the set of behaviors that another may adopt (e.g., Wallot et al., 2016) or intermittent coordination, where people move in and out of coordinated states (Dahan et al., 2016; Nowak et al., 2017; Mayo and Gordon, 2020), such as the mother-infant interactions, which tend to include short periods of shared emotional activity as well as states where one or both partners show no interest in interacting with the other (see Kokkinaki et al., 2017); or scenarios in which social exchanges over time are characterized by qualitatively distinct phases of coordination (i.e., phase transitions), such as collaborative problem solving (Wiltshire et al., 2018) or psychotherapy (García and Di Paolo, 2018). More research in this area could help us understand to what extent these dynamics have confounded synchronization experiments in the literature and, more importantly, what is their contribution to the rhythmic pattern at the group-level: do the mismatched emotional states in mother-infant dyads have fractal-like temporal structure? Are the different phases of coordination characterized by different patterns of dimensional compression?

Relationship to a Collective Feeling of Wellbeing and Connection

To our knowledge, there is no experimental evidence confirming how an emergent collective rhythm could be related to a collective feeling of wellbeing and connection, only correlational evidence found in the anthropological literature between collective activities and group cohesion, ecstasy, wellbeing, and solidarity (reviewed in Gelfand et al., 2020), such as marching together during military drills (McNeill, 1997: 2), the church services in early Christian practices (Ehrenreich, 2007: 65) or secular festivities during the Middle Ages (Ehrenreich, 2007: 92).

Confirmation of an emergent collective rhythm and its relationship to a collective sense of wellbeing could lead to a more straightforward explanation to the previously suggested association (Haidt et al., 2008; Wheatley et al., 2012; Mogan et al., 2017; Wood et al., 2018; Clayton et al., 2020) between collective coordination and what Emile Durkheim coined as "collective effervescence," i.e., the feeling of belonging and assimilation experienced during collective rituals (cited in Xygalatas et al., 2011). Additionally, evidence in this regard would be compatible with the "hive hypothesis" (Haidt et al., 2008: 136) which builds on Durkheim's collective effervescence and states that "people need to lose their selves occasionally by becoming part of an emergent social organism (. . .) and in which self-consciousness is greatly reduced and one feels merged with or part of something greater than the self." Put differently, group dynamics could provide a common beat to which to coordinate, thereby overcoming individual rhythms (Wheatley et al., 2012). According to the evidence presented so far, a collective rhythm analogous to a musical beat would emerge from, at least, the accommodation of bodily states, would disperse depending on the participants' interconnection structure (either by sensory perception, affiliative connection, cultural preferences) and, analogous to dyadic interactions, would facilitate feelings of connection and assimilation to the group, and contagious euphoria.

Evidence supporting these hypotheses comes from a pair of studies of a fire-walking ceremony in a Spanish village (Konvalinka et al., 2011; Xygalatas et al., 2011). The results show that, compared to non-related pairs, the heart rates of firewalkers and related spectators share similar temporal dynamics, such as a more structured pattern and a peak distributed around the fire-walk. Moreover, this shared pattern extended through a network from related to unrelated performers. These findings suggest that during a collective ritual, the coordination of bodily states may be constrained by the social network of the participants and that the resulting rhythmicity will relate to the activities that take place in it. Although only a few studies have addressed the influence of the network topology on the collective rhythm, they have shown that the level of coordination varies depending on the pattern of interconnections (i.e., topology) among participants (van de Rijt, 2018), and their internal tempo (Alderisio et al., 2017). Methods specifically designed to capture changes in network modularity over time could help elucidate, for example, whether the complementary dynamics observed during joint action (e.g., Wallot et al., 2016) can be seen as a small-scale instance of a modular organization subjected to certain environmental constraints and contingencies (see Bourbousson and Fortes-Bourbousson, 2016; Mayo and Gordon, 2020), and to what extent the intermittent coordination that results from such modularity contributes to the complexity and fluency of the collective temporal pattern.

Confirmation on the relationship between an emergent collective rhythm and a collective feeling of wellbeing could be of clinical relevance, as some disorders or impairments might target different aspects of the causal model presented in **Figure 3**. For instance, patients with autism spectrum disorder (i.e., endogenous rhythms: Bobin-Bègue, 2019) and people with decreased complexity of locomotion due to aging (i.e., locomotor rhythms: Almurad et al., 2018) have disruptions of individual rhythms. People with schizophrenia (Varlet et al., 2012) and social anxiety disorder (Varlet et al., 2014) have shown disrupted coordination dynamics in leader-follower interactions when the patient had to lead the coordination, but unaffected dynamics in unintentional coordination. Understanding how the collective rhythm emerges from the constraints and contingencies at different levels (e.g., individual vs. interaction level) could help develop intervention strategies that include not only patients but the people interacting with them, to improve their social exchange. For example, in addition to protocols that help patients with social anxiety disorder to manage their leader position during an interaction, these patients could benefit from social exchanges where no agent controls the social dynamic, i.e., the type of interaction that could lead to an emergent collective rhythm. Or patients with disruptions of locomotor rhythms could benefit from group activities where they synchronize their movements to evenly spaced rhythms.

Artificial Manipulation of the Collective Rhythm

It remains to be seen whether a collective rhythm emerges during group activities and to what extent it is related to the collective effervescence experience and the hive hypothesis. However, a plausible example of the artificial manipulation of the collective rhythm according to the sociocultural context, is the link between ritualistic synchrony and the theory of cultural evolution known as tightness-looseness theory (Gelfand et al., 2020). According to this theory, in order to survive, societies marked by higher rates of socioecological threats like natural disasters or food insecurity tend to develop tighter cultural norms than those with fewer coordination needs. In that particular context, the effects of ritualistic synchrony would be adaptive, given that in the face of greater threats, the benefits (i.e., cooperation, coordination, cohesion) of synchronized activities such as dancing, chanting or marching, would outweigh the negative effects (e.g., less creativity) associated with them. Within this framework, Gelfand et al. (2020) predict that the use of synchrony in ritualistic scenarios would be common after periods that require social coordination, such as after ecological or social threat. This prediction needs to be further investigated, but it is concordant with the argument that humans artificially manipulate the effects of interpersonal coordination at a collective level according to the needs of the sociocultural context.

Overall, research on this topic would help to explain anthropological research (reviewed in McNeill, 1997; Ehrenreich, 2007; Haidt et al., 2008) showing, for instance, that although the degree of synchronized physical activity observed changes over the years and between social groups, the feeling of connection remains; it could also improve our knowledge of derived human traits with fixed (e.g., music) and labile (e.g., storytelling) tempo.

Concluding Remarks

During group activities, the interpersonal coordination at different levels and modalities gives a temporal structure to the collective dynamics. The evidence suggests that this phenomenon facilitates the emergence of a collective rhythm, i.e., temporal regularities that cannot be predicted from the individual periodicities, and that this group-level property could be related to a collective feeling of wellbeing and connection. Although more research is needed to test this argument, we highlight two ways of obtaining a clearer picture of the complexity associated with social coordination at the collective level. First, it is important to take into account that behavioral dynamics go beyond simple synchronization. Developing methods, including experimental settings, that explore complex and multilayered social dynamics with, for example, compensatory exchanges or intermittent coordination, may clarify their influence on the construction of a collective rhythm and its consequences.

Second, our framework naturally incorporates the variability of the social consequences of interpersonal coordination. We suggest that the study of the social effects of interpersonal coordination should highlight that in the early stages of life these are important for the survival, homeostasis, and adaptation of the child to a dynamic physical and social environment. Later in life, it should be emphasized that these effects are shaped by the constructed niche (biological and sociocultural) in which the individual developed and the social constraints in which the interaction takes place. Overall, our understanding of how these evolutionary social effects of interpersonal coordination have been adapted to the constructed environment would be improved with studies in which artificial experiments (e.g., finger tapping) are applied to non-WEIRD participants (i.e., people from Western, educated, industrialized, rich and democratic societies), and with studies in more naturalistic settings that include the variety of cultural practices in which social coordination fosters feelings of cohesion and collective effervescence.

AUTHOR CONTRIBUTIONS

AF and GR-F jointly conceived, designed, and revised the manuscript. AF wrote the first draft of the manuscript. Both authors contributed to the article and approved the submitted version.

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REVIEW
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Sensorimotor Synchronization in Healthy Aging and Neurocognitive Disorders

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Sensorimotor synchronization (SMS), the coordination of physical actions in time with a rhythmic sequence, is a skill that is necessary not only for keeping the beat when making music, but in a wide variety of interpersonal contexts. Being able to attend to temporal regularities in the environment is a prerequisite for event prediction, which lies at the heart of many cognitive and social operations. It is therefore of value to assess and potentially stimulate SMS abilities, particularly in aging and neurocognitive disorders (NCDs), to understand intra-individual communication in the later stages of life, and to devise effective music-based interventions. While a bulk of research exists about SMS and movement-based interventions in Parkinson's disease, a lot less is known about other types of neurodegenerative disorders, such as Alzheimer's disease, vascular dementia, or frontotemporal dementia. In this review, we outline the brain and cognitive mechanisms involved in SMS with auditory stimuli, and how they might be subject to change in healthy and pathological aging. Globally, SMS with isochronous sounds is a relatively well-preserved skill in old adulthood and in patients with NCDs. At the same time, natural tapping speed decreases with age. Furthermore, especially when synchronizing to sequences at slow tempi, regularity and precision might be lower in older adults, and even more so in people with NCDs, presumably due to the fact that this process relies on attention and working memory resources that depend on the prefrontal cortex and parietal areas. Finally, we point out that the effect of the severity and etiology of NCDs on sensorimotor abilities is still unclear: More research is needed with moderate and severe NCD, comparing different etiologies, and using complex auditory signals, such as music.

Keywords: aging, dementia, rhythm, finger tapping, timing, Alzheimer's disease, music, neurodegenerative diseases

INTRODUCTION

Sensorimotor synchronization (SMS) is defined as temporal coordination of a motor rhythm with an external rhythm. It is a form of adaptive interaction with the environment (Schwartze et al., 2011). Being able to synchronize to regularities in temporal structure and matching one's movements to those of others is of obvious importance in activities whose essence is based on creating a shared temporal structure, such as dance or joint music making (Sebanz et al., 2006). However, organizing one's own behavior according to the dynamic unfolding of events in the environment is crucial to many more situations than that. Interpersonal entrainment is a key rhythmic feature in human interactions, including non-musical interactions (Bispham, 2006). Many situations that do not require synchrony nonetheless cause people to synchronize their movements to each other, such as when people unintentionally synchronize their postural sway (Shockley et al., 2003) or lower limb movements while walking (van Ulzen et al., 2008; Nessler and Gilliland, 2010), or entrain the frequency of their movements to each other while clapping hands. While the use of a pulse in structuring one's behavior in time is self-evident in musical activities in which the goal is to maintain temporal stability, a pulse also appears in a more loose and subconscious way in interpersonal turn-taking interactions (Bispham, 2006). Spoken language contains remarkable temporal regularities in the signal envelope of the produced acoustic signal, as well as in vocal tract movements and syllable duration and rate (Poeppel and Assaneo, 2020). When comparing linguistic groups, correlations between aspects of temporal structuring in music emerge (Patel and Daniele, 2003) underscoring the universality of attending to regularities in auditory signals generally. Dynamic attending theory (Jones, 1976; Large and Jones, 1999) proposes that when presented with an auditory sequence, listeners' attention will oscillate periodically such that it is higher on the beat than off the beat, to allow for optimal processing and forming the basis for prediction. Although dynamic attending theory has mainly been used to explain phenomena of rhythmic perception in relation to sequences that are musical or isochronous (i.e., periodical with a constant interval between beats), it has also been proposed to explain interactional synchrony between people that happens in a less strictly rhythmic fashion (Cason et al., 2017). While language does not follow an isochronous rhythm, it is nonetheless based on temporal regularities, facilitating understanding by allowing the listener to predict incoming auditory input (Byrd and Saltzman, 2003; Port, 2003). In a domain-general fashion, entrainment to regular auditory input may thus enhance the representation of regularities in sound, guiding one's attention to point in time at which meaningful information is being delivered (Obleser and Kayser, 2019; Mathias et al., 2020). Accordingly, the perceptual system appears to be tuned to the natural rhythm of speech (frequencies between 2 and 8 Hz; Poeppel and Assaneo, 2020) Contrariwise, problems to perceive regularities in the environment and tune one's attention to them might hamper interpersonal communication. Indeed, it has been demonstrated that an inability to perceive a beat in music generalizes to a weakness in perceiving periodicities in speech (Lagrois et al., 2019). In other words, measuring a person's ability to perceive and synchronize with rhythms in the environment does not only reveal that person's sense of rhythm, but a more general propensity to predict events in the environment and relate to others.

It is therefore worthwhile to assess and study SMS abilities. However, the effect of age and neurocognitive disorders (NCDs) on sensorimotor abilities remains understudied. NCDs are a growing health concern to which an effective treatment remains elusive. Besides cognitive decline and degradation of memory performance, a common consequence of this condition is a decrease in the quality of social relationships. Decreased interactions with others and the environment is common to patients with dementia (Colling, 2000), a potential result of sensory decline common to old age (Gates and Mills, 2005; Correia et al., 2016) and to NCDs (Armstrong, 2009; Hardy et al., 2016; Brenowitz et al., 2019), or a consequence of living in isolation or in an inpatient context with insufficient social stimulation (Chung, 2004; Kolanowski et al., 2006). Nonetheless, this impairment in communication might also be understood as an impairment in the detection of regularities in the environment (Hoehl et al., 2021). Stimulating and training someone's sensorimotor abilities might inadvertently restore their capacity to predict events in the environment, and to relate successfully to others.

Music-based interventions, which are increasingly suggested in the treatment of NCDs [Guideline Adaptation Committee, 2016; National Institute for Health and Care Excellence (NICE), 2019], might reach their peak of effectiveness if they successfully stimulate SMS (Ghilain et al., 2019; Hobeika and Samson, 2020), particularly in those individuals whose motor abilities remain relatively unimpaired despite decline in other domains. Music-based interventions exist in many forms but those that encourage active participation appear to bring greater benefits on behavioral and psychological variables than those in which patients listen passively (Sakamoto et al., 2013; Särkämö et al., 2014), suggesting an important role of SMS in the effectiveness of these interventions. First, moving in time with others has been shown to promote feelings of social cohesion, prosocial attitudes, and cooperative behavior (Wiltermuth and Heath, 2009). Second, temporal expectations elicited by the perception of a musical beat may stimulate the reward network and induce pleasure (Salimpoor et al., 2011). Improving a person's temporal prediction abilities might help them synchronize and interact with others (Pecenka and Keller, 2011), and therefore improve communication and reduce isolation.

At present, motor abilities have been well examined in patients with Parkinson's disease (Grahn and Brett, 2009; Dalla Bella, 2018) but studies investigating SMS skills in other neurological diseases (notably NCDs) are scarce. Even in the case of healthy physiological aging, little consensus exists in the literature as to whether sensorimotor skills are preserved in old age. With this review, we aim to shed light on the question of how SMS abilities develop in the late decades of life and over the course of NCDs. Additionally, we touch upon the possibility of using SMS as a diagnostic tool. Since NCDs are afflictions of the aging brain, it is important to disentangle NCD-related changes in SMS from those related to healthy aging. Throughout this review, we will use the terms major and mild NCD. Major and mild NCD are the current terms used in the *Diagnostic and Statistical Manual of Mental Disorders* (5th ed.; DSM-5; American Psychiatric Association, 2013) for what is otherwise referred to as dementia and mild cognitive impairment (MCI). Although technically NCD is a somewhat broader term, for example including cognitive impairment in young people caused by traumatic brain injury or HIV infection, we will use the term NCD when discussing studies that themselves might have used the terms dementia or MCI in their nomenclature. In any case, all studies about NCDs reviewed here involved elderly subjects. Finally, Parkinson's disease is often discussed in the context of NCDs, and indeed "major/mild NCD [possibly] due to Parkinson's disease" exist as conditions in the DSM-5. However, Parkinson's disease is primarily a movement disorder, and as such, there already exists a bulk of literature regarding motor abilities in this population (Grahn and Brett, 2009; Grabli et al., 2012) as well as the use of rhythmic stimulation in rehabilitation (Dalla Bella et al., 2017a; Cochen De Cock et al., 2018; Dalla Bella, 2018), so we do not wish to add to this literature and restrict our review to the other, mostly cortical, etiologies of NCD, such as Alzheimer's disease (AD), vascular NCD, or NCD with multiple etiologies.

Our review is therefore organized as follows: First, after clarifying what is meant by SMS and how it is quantified and assessed, we present the cognitive and brain mechanisms that lie at the heart of SMS, in general terms and as a function of the more specific task requirements. Next, we give an overview of how the aging process influences cognitive performance and brain structure and function, followed by a section on how these processes are influenced by NCDs. In both cases, we offer some predictions with regard to SMS performance. We then review the available literature on SMS in healthy aging, followed by the literature on SMS in NCDs to evaluate the predictions we made. We conclude with some suggestions for future research.

Sensorimotor Synchronization: Common Paradigms and Ways of Assessing Performance

Synchronizing one's movement with an external rhythm can come in many forms including moving one's limbs with an auditory sequence, walking, or dancing (Repp and Su, 2013). However, the most commonly employed paradigm is that in which a participant is asked to produce regular, rhythmic taps with a finger. In the context of this review, we refer to two main types of tapping paradigms as unpaced tapping and paced tapping. Unpaced tapping corresponds to tasks in which participants produce movements at a self-generated rate, very often to identify someone's spontaneous motor tempo (SMT) but also to assess how fast or slow one can maintain a regular rate. Paced tapping, on the other hand, consists of synchronizing one's tapping to an auditory pacer. This pacer can be a simple isochronous (metronomic) sequence, with the goal to match each tap to the onset of each beat, but it can also be a more complex stimulus (such as music) where the beat must be inferred. Very often, the participant continues to do this until the signal fades, a case to which we refer as *synchronization without continuation*, to distinguish it from *synchronization–continuation*, that is, tasks in which participants first synchronize their tapping with an auditory pacer, but then continue tapping at the same speed for some time after the stimulus has faded.

Sensorimotor synchronization performance measured by these tasks is described in terms of variability and accuracy. When the participant synchronizes to an external metronome or rhythmic stimulus, accuracy or beat alignment refers to the extent to which taps occur before (negative asynchrony) or after (positive asynchrony) the beat (event onset in the external rhythm) and is thus expressed as a difference in ms. Variability or precision refers to the standard deviation of the asynchronies. On the other hand, during continuation tapping, the main observable is the inter-tap interval (ITI), and its average and standard deviation are reported. Mean ITI reflects whether the subject drifts away from the original tempo, while ITI variability, or precision, refers to how consistently an individual's taps are distributed around a period and is given by the standard deviation (SD) of the ITIs within a trial, or the coefficient of variation (CV; SD divided by mean ITI). Sometimes, variability is expressed as its inverse, consistency. Finally, mean ITI (reflecting average speed) and ITI variability are also used as outcomes in self-paced tapping, in the absence of an external stimulus.

BRAIN AND COGNITIVE MECHANISMS INVOLVED IN SENSORIMOTOR SYNCHRONIZATION

Which brain networks are involved in SMS tapping depends on the exact nature and instructions of the task, but very generally, areas involved in tapping tasks are primary sensory and motor cortices, supplementary motor area (SMA), anterior cerebellum, dorsolateral prefrontal cortex, premotor cortex, parietal areas, and the basal ganglia (Larsson et al., 1996; Rao, 1997; Penhune and Doyon, 2005; Molinari et al., 2007; Chen et al., 2008; Witt et al., 2008; Kung et al., 2013; Repp and Su, 2013). Another general observation that can be made across a variety of timing tasks is that there seem to be two somewhat disparate networks for processing intervals depending on the length of the inter-onset interval (IOI; Repp and Su, 2013). The automatic timing network is involved in the processing of sub-second intervals and includes the primary motor cortex, the SMA, the premotor cortex, and the cerebellum (Lewis and Miall, 2003). The cognitively controlled timing network is involved in the processing of intervals longer than 1 s. It comprises areas of the parietal cortex, prefrontal cortex, and the basal ganglia (Lewis and Miall, 2003; Buhusi and Meck, 2005; Koch et al., 2009; Coull et al., 2011, 2013; **Figure 1**).[1] The basal ganglia, universally involved in beat processing (Grahn, 2009), are also considered part of the automatic timing network by some (Lewis and Miall, 2003; Koch et al., 2009), but not all authors (Buhusi and Meck, 2005), although, as Coull et al. (2011) point out, it may well be that different nuclei within the basal ganglia are responsible for timing in the sub- and supra-second range, respectively. Contrary to the

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[1] https://www.nitrc.org/projects/mricrogl/

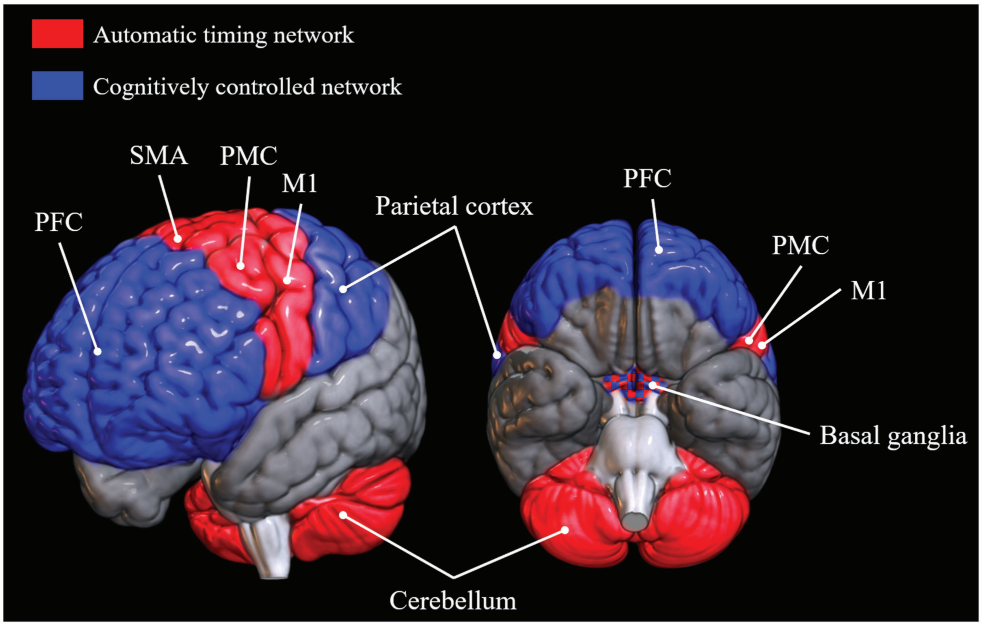

FIGURE 1 | Brain areas reported to be active in tasks requiring automatic timing and cognitively controlled timing, respectively (Lewis and Miall, 2003; Buhusi and Meck, 2005; Koch et al., 2009; Coull et al., 2011, 2013; Repp and Su, 2013). Brain networks were plotted onto a standard MNI152 template rendered with the open-source software MRIcroGL (McCausland Center for Brain Imaging, University of South Carolina). PFC, prefrontal cortex; SMA, supplementary motor area; PMC, premotor cortex; M1, primary motor cortex.

automatic timing network, the cognitively controlled timing network is based on brain areas involved in high-level cognitive functions. Indeed, Coull et al. (2011, 2013) suggest that explicit estimation of current stimulus duration is a conscious cognitive operation necessary to perceive periodicity in a slow stimulus with an interval length of above around 1 s. In a related manner, for the successful perception of and synchronization to a slow beat, people might employ tactics, such as explicit counting (Grondin et al., 1999) and/or subdivision of the given interval (Repp, 2003; Repp and Doggett, 2007), strategies that arguably rely more on attentional and memory processes and corresponding brain networks and less on pure more mechanisms and structures. According to Koch et al. (2009), the dorsolateral prefrontal cortex's role in the timing of long intervals might be related to WM. A study by Henley et al. (2014) supports this idea, as they observed correlations between the ability to maintain a slow beat and their WM capacity, measured with the digit span backwards test (Wechsler, 1981).

Unpaced Tapping

As mentioned in the previous section, unpaced tapping tasks are frequently in such a manner that one's natural, SMT is measured. SMT tends to be consistent across repeated measures within the same participant and is seen as a reliable metric of internal tempo or clock (Denner et al., 1964). In addition, one might look at preferred perceptual tempo, which is a perceptual analogue to SMT.

In cognitive terms, results of spontaneous tapping studies have been explained in terms of an internal clock mechanism. Many authors have argued that people possess an internal clock which determines not only at which tempo they comfortably synchronize their movements, but also their ability to predict how events in the environment unfold over time (McAuley et al., 2006; Turgeon and Wing, 2012). Such an internal clock is often conceptualized as a pacemaker emitting pulses and a reference memory evaluating time by counting the number of pulses emitted (Church, 1984).

Some evidence suggests that tapping at a self-determined speed, as opposed to synchronizing one's movement with an external pacer, engages particularly the primary motor cortex, premotor cortex, SMA, dorsolateral prefrontal cortex, as well as areas of the parietal lobe and cerebellum (Larsson et al., 1996; Witt et al., 2008). Furthermore, a lesion study involving patients with basal ganglia pathology also demonstrated that self-paced tapping may depend on basal ganglia integrity, as patients tapped at more heterogeneous rates and with increased variability compared to healthy controls (Schwartze et al., 2011). The authors posit that self-paced tapping might specifically depend on the integrity of connections between pre-SMA and striatum.

Besides paradigms to identify a person's SMT, unpaced tapping can also take the form of tasks in which participants tap as fast or as slow as possible while maintaining a continuous regular rhythm. Tapping at a fast rate might engage the same automatic timing network, but might additionally depend on factors like the time required for muscle contractions and muscular and joint flexibility (Daley and Spinks, 2000; Carmeli et al., 2003). However, synchronization precision at a very fast tempo might additionally require attentional resources, as suggested by a study that found a correlation (Colella et al., 2021) between variability of tapping and score on the Frontal Assessment Battery, a test of frontal lobe integrity said to reflect attention (Dubois et al., 2000). Tapping at a very slow rate, on the other hand, might involve a conscious representation of the current interval and a memory aspect, likely implicating structures from the cognitively controlled network (**Figure 1**).

Paced Tapping

As mentioned above, we distinguish between simple synchronization tasks without continuation and synchronization–continuation paradigms. The former type of task is expected to engage the motor circuitry associated with timing tasks, such as motor cortical areas, cerebellum, and basal ganglia, with some studies suggesting even stronger involvement of the premotor cortex and cerebellum with such externally paced movement than when a tempo is internally maintained (Del Olmo et al., 2007; Kornysheva and Schubotz, 2011), like in the continuation phase of synchronization–continuation tasks. While a few studies suggest the same areas to be involved in continuation as in synchronization (Jäncke et al., 2000; Jantzen et al., 2004), continuation tapping after an external stimulus has faded might elicit additional activation in primary sensory and motor cortices (Gerloff et al., 1998), premotor cortex, SMA (Serrien, 2008), thalamus, and basal ganglia (specifically, putamen; Lewis et al., 2004). One study also demonstrated that a prefrontal–parietal–temporal network, containing the dorsal and ventral prefrontal cortex, middle temporal gyrus, and parietal lobes, may be especially activated during continuation tapping (Jantzen et al., 2007). The authors suggest that the involvement of the prefrontal cortex reflects the task's requirement to form an internal representation of the sequence tempo and to recruit attentive processes. This is supported by a study finding prefrontal white matter integrity to be related to variability of tapping in the continuation phase of a synchronization–continuation task (Ullén et al., 2008).

Just like for unpaced tapping, the exact involvement of brain networks and cognitive mechanisms may vary depending on sequence tempo in tasks involving synchronization with and without continuation alike. Accordingly, we can expect particular recruitment of structures like the prefrontal cortex and the parietal lobes (the cognitively controlled timing network) in paced tapping at speeds beyond 1 s (Koch et al., 2009).

BRAIN AND COGNITIVE CORRELATES OF HEALTHY AGING AND NEUROCOGNITIVE DISORDERS

Healthy Aging

Even in the absence of neurodegenerative disease, the aging brain is subjected to global cortical atrophy and loss of functional integrity. Particularly affected structures are the frontal lobes (Kaup et al., 2011) and the hippocampus (Persson et al., 2006). Reduced cortical volume has also been demonstrated in the parietal cortex (Kalpouzos et al., 2012), and functional connectivity between parietal regions and prefrontal cortex has been shown to be reduced in aging (Madden et al., 2010). With these structures impacted in old age, it is not surprising that aging is associated with deficits in WM and attention in particular (Grady, 2012; Harada et al., 2013). Conversely, genetic markers of aging have been shown to accumulate more slowly in the cerebellum than in other parts of the brain (Liang and Carlson, 2020). Given the cerebellum's role in precise motor timing (Bastian, 2006; Bares et al., 2007), this points to a possible preservation of timing abilities in old age. Additionally, the motor cortex does not belong to the heavily impacted structures in normal aging, but some atrophy in motor cortical regions has been observed, together with atrophy in the corpus callosum (Seidler et al., 2010). Functional neuroimaging has found different patterns of brain activation in motor tasks between older and younger people. More specifically, some motor tasks (especially fine motor control) engage motor regions in everyone, but additionally engage prefrontal and sensorimotor networks in aged people (Heuninckx et al., 2005, 2008; Seidler et al., 2010), even in cases where there are no age-related differences in performance. This might reflect a shift from more automatic to more controlled processing with age, in spite of the same task instructions and the same outcome (Heuninckx et al., 2005). In line with those results. a resting-state functional connectivity study also found a pattern of heightened connectivity in some motor networks (motor cortex and cerebellar lobule VIII with putamen) and decreased connectivity in others (cerebellar lobule V and VIII with sensorimotor portion of insular cortex; Seidler et al., 2015). All these results might point to a mechanism of compensation, in which motor cortex pathology in old age is offset by an additional use of other domain-general neural resources, among others in the prefrontal cortex. This might also explain relations between sensorimotor function and cognitive functions in age (Li and Lindenberger, 2002). If motor tasks rely more on prefrontal cortex and other networks in old age, we would assume a covariation of motor performance and cognitive functions, and competition of resources if a task involves both motor and cognitive requirements. Alternatively, the additional involvement of non-motor regions in older people might also reflect a less efficient use of neural resources in older people (Stevens et al., 2008; Grady, 2012).

This picture of age-related changes in cognitive functions and neural mechanisms generates some predictions. If we imagine internal clock in terms of a pacemaker emitting regular pulses and a person's SMT as "one tap every *n* pulses," and if we suppose that internal clock slows with age, as has often been suggested (Vanneste et al., 2001; Turgeon and Wing, 2012), this means that the rate of regularly emitted pulses is lower with age. Consequently, SMT and preferred perceptual tempo should be lower with age, but we do not have a reason to believe that people would tap spontaneously with a higher variability. If one chooses their own tempo and provides one tap every *n* pulses, even if these pulses occur less frequently, variability is not expected to be affected. On a cerebral level, the relative preservation of cerebellar integrity (Liang and Carlson, 2020) also suggests preserved variability in spontaneous tapping, given the cerebellum's role in predictive movement control (Bastian, 2006). However, on fast unpaced tapping tasks, we expect a slower speed as well as reduced consistency. As mentioned above, CV when tapping as fast as possible has been linked to attention (Colella et al., 2021), and we expect lower available attentional resources in aging to be reflected in lower consistency.

Regarding paced tapping, due to the relative preservation of cerebellum and motor cortical structures in aging, we do not expect a great decline in performance in elderly people, at least at intervals that are neither very fast nor very slow, except perhaps for very old people. With regard to synchronization to very fast stimuli, we might imagine lower consistency. If an internal pacemaker emits fewer pulses with age, this should lead to a reduced temporal resolution of perceived stimuli and therefore increasing difficulty to synchronize to them as interval length decreases. Conversely, due to the asserted use of the cognitively controlled timing system with very slow intervals (above 1 s), we would expect differences in brain activation with aging. As the memory and attentional resources might already be used for fundamental motor synchronization due to compensatory rewiring, we hypothesize a larger involvement of parietal areas and prefrontal cortex to fulfill those requirements, and/or a decrease in performance.

Neurocognitive Disorders

In order to describe the neuropathology of NCDs and make predictions regarding SMS in cognitively impaired people accordingly, it is important to acknowledge that NCD is a complex clinical picture that can have several different etiologies, including AD, vascular NCD, frontotemporal NCD, NCD with Lewy bodies, and others.

Most of the brain structural damage in NCDs, especially in AD, occurs in the hippocampus and surrounding parietal–temporal areas, even in early stages of the disease (Braak and Braak, 1991; Scheff et al., 2006; Jacobsen et al., 2015; Rémy et al., 2015). Besides the hippocampus, there is reduced structural and functional integrity in the prefrontal cortex (Braak and Braak, 1991; Rémy et al., 2015). WM and attention capacity are reduced, beyond what is usual with healthy aging. Conversely, primary sensory, motor, visual and anterior cingulate cortices are relatively well preserved (Jacobsen et al., 2015). However, despite cortical atrophy affecting some structures more than others, the entire cortex is affected and particularly in late stages of the disease, motor areas show the same neurofibrillary tangles and neurotic plaques as other areas, as some autopsy studies reveal (Golaz et al., 1992; Suva et al., 1999). Some research even suggests that motor cortex atrophy occurs in early stage NCD, although motor symptoms are visible only in later stages of the disease. Similarly to healthy aging, there is some evidence for compensatory processes: One study reported hyperexcitability of the sensorimotor cortex in AD patients compared to age-matched controls, even in the absence of motor symptoms (Ferreri et al., 2016). A diffusion tensor imaging study demonstrated some rewiring with alternative connectivity between motor cortex and other cortical and subcortical areas in AD and MCI (Agosta et al., 2010). Additionally, this level of rewiring was correlated with hippocampal atrophy and AD-related changes in grey matter volume. It is conceivable that these NCD-related changes reflect an attempt to compensate for degeneration of motor structures by employing additional brain networks to perform motor tasks.

Even AD can be considered a somewhat heterogeneous disease that could possibly be further divided into subtypes (Lam et al., 2013). In vascular NCD, the second most common type, the brain damage depends on the location of the vascular accident. It can be primarily cortical, primarily subcortical, or a combination, and the neuropsychological profile is accordingly variable (Braaten et al., 2006; O'Brien and Thomas, 2015). In short, NCD is a diverse clinical picture, and even its subtypes can further be divided into subcategories, so it is difficult to make predictions with regard to SMS performance. The following predictions, as well as the results discussed later, might to some extent be generalizable, but apply to AD patients more than to people with other NCDs.

Generally, there is not too much evidence to suggest that people with NCDs would perform worse on unpaced tapping tasks. However, given that self-paced tapping has been shown to depend more on dorsolateral prefrontal cortex and parietal lobe integrity (Witt et al., 2008), it could be that accuracy and consistency might be lower in people with NCDs. Additionally, it must be mentioned that unpaced tapping might be differently affected by different patterns of neural degeneration. For example, basal ganglia pathology is particularly associated with vascular NCD (Hansen et al., 2015; Banerjee et al., 2017), so maybe people with vascular NCDs, and particularly those with damage to the basal ganglia, might be more impacted in unpaced tapping tasks, which may rely more heavily on basal ganglia (Schwartze et al., 2011), as discussed above.

Regarding paced tapping tasks, as with healthy aging, the degree to which people with NCDs might be impaired might especially depend on interval length. Since motor structures, including the cerebellum, are relatively well preserved in people with NCDs, we expect relatively good performance when using the automatic timing network, that is, at fast and comfortable intervals, and especially at tasks using synchronization without continuation, that is, without a requirement to create a mental representation of a given interval. We might expect some difficulty, reflected in higher variability in people with NCDs compared to healthy participants on synchronization–continuation tasks, since continuation tapping involves WM and structures like the prefrontal cortex, parietal and temporal lobes are implicated, all of which are more impacted in NCDs than in healthy aging. Besides higher variability, we hypothesize people with NCDs to speed up on continuation tapping at slow tempi, given that speeding up on such tasks has previously been related to performance on WM tasks (Henley et al., 2014). We could conjecture that tapping at slow tempi would be even more impaired in people with frontotemporal NCD, since here the prefrontal cortex is especially impaired. Perhaps strategies like explicit counting and subdivision that can help people to synchronize with slow sequences are also less utilized by people with NCDs than by their healthy counterparts.

TABLE 1 | Studies investigating spontaneous motor tempo in different age groups.

Study		Young	Middle-aged	Old	Very old
Baudouin et al. (2004)	*n*	20	–	21	21
	M_{Age} (SD)	25.05 (3.71)		73.19 (4.54)	85.90 (3.32)
	SMT in ms (SD)	654^{***a} (186)		1,072^{***a} (318)	1,125^{***a} (426)
McAuley et al. (2006)	*n*	119	52	25	21
	Age range	18–38	39–59	60–74	75–95
	SMT in ms (SD)	630^{**b} (22)	522^{**b} (34)	632^{**b} (59)	648^{**b} (43)
Age significantly predicted SMT**					
Turgeon and Wing (2012)	*n*	60			
	M_{Age} (SD_{Age})	54.35 (25.18)			
	SMT				
Age significantly predicted SMT***					
Vanneste et al. (2001)	*n*	8	–	11	–
	M_{Age} (SD)	26.25 (1.83)		69 (4.52)	
	SMT in ms (Range)	536** (283–727)		747** (625–1,035)	

M, mean; SD, standard deviation; SMT, spontaneous motor tempo. [a]*Old and very old groups significantly different than young group; no difference between old and very old.* [b]*No statistical test for between-group differences was performed, but a regression analysis found age to significantly predict SMT.* $^{**}p<0.01$; $^{***}p<0.001$.

SENSORIMOTOR SYNCHRONIZATION IN HEALTHY AGING

In the following, we discuss and synthesize some of the relevant research that features tasks that make people of different ages tap in a rhythmic fashion, to test the predictions we made. We report separately on unpaced and paced tapping tasks, which both contribute complementary information about how temporal mechanisms change with age. Previous research has demonstrated that people (regardless of age or cognitive impairment) spontaneously produce intervals of around 600 ms (Dalla Bella et al., 2017b) and that synchronization to external rhythms is best between 400 and 800 ms (McAuley, 2010), thus suggesting a relationship between these two measures in the sense that synchronization consistency and accuracy may become smaller as the difference between target tempo and internal tempo becomes greater.

Unpaced Tapping

Spontaneous Motor Tempo

Studies that have compared SMT across age groups generally agree with each other in that they find a significantly slower tempo in older compared to younger people (Vanneste et al., 2001; Baudouin et al., 2004; McAuley et al., 2006; Turgeon and Wing, 2012; see **Table 1**). It is merely the magnitude of slowing with age, as well as the exact developmental course, that were somewhat different across studies. For example, while some studies found quite substantial differences in the ITIs of participants of different ages (1,072 ms for old participants; 654 ms for young participants; Baudouin et al., 2004), this difference is smaller in other studies (747 ms in old participants; 536 ms in young participants; Vanneste et al., 2001) and even subtler in others (McAuley et al., 2006, found the SMT of people aged 75+ to be 648 ms, 632 ms for participants between 60 and 74, and 522 ms for people aged 39–59).

Regarding the developmental course, some authors demonstrated that it is especially in very old age that a slowing of SMT is visible. McAuley et al. (2006) found a cubic relationship between age and SMT, suggesting that this variable slows particularly late in life (i.e., after the age of 75). Similarly, in study of Turgeon and Wing (2012), a slowing of spontaneous motor rate was visible particularly in participants aged 75 and above.

Consistency of spontaneous tapping, which is usually expressed in terms of CV, does not appear to be as affected by age, as we predicted. McAuley et al. (2006) and Vanneste et al. (2001) found that old and very old people at their preferred tempo tapped as consistently as young ones. Along similar lines, using linear regression, Turgeon and Wing (2012) did not find age to predict a significant proportion of variance of CV. Thus, at a tempo that participants choose themselves, differences in terms of consistency have not been observed between young and old people.

As SMT reflects one's natural rate of rhythmic motor activity, it is often thought of as being related to preferred perceptual tempo. McAuley et al. (2006) investigated the relationship between SMT and preferred perceptual tempo, in a study in which they presented rhythmic sequences of different speeds to their participants and asked them to judge whether each sequence was too fast, too slow, just right (relative to their favorite speed), or anything in between. They found that preferred perceptual tempo slowed with age along with SMT and that these two variables were highly correlated. One may then conclude that SMT, which appears to significantly slow down with age, might reflect the slowing of one's internal clock in old age.

Fastest and Slowest Unpaced Tapping

Other types of unpaced tapping are those that require participants to tap in a repeating, continuous fashion as fast or as slow as possible, to see at which upper and lower limit participants are able to maintain a regular tap. As demonstrated by a large number of studies, when given the instruction to tap regularly

TABLE 2 | Studies investigating paced tapping in different age groups.

Study		Fast tempo (<350 ms)		Comfortable tempo		Slow tempo (>1,000 ms)	
		IOI	Age effect	IOI	Age effect	IOI	Age effect
Bangert and Balota (2012)	Consistency	–		500 ms/1,000 ms	No diff.	1,500 ms	O<Y***
	Accuracy				No diff.		O<Y*
Carment et al. (2018)	Consistency	333 ms	No diff.	500 ms/1,000 ms	No diff	–	
	Accuracy		O<Y***		No diff.		
Drewing et al. (2006)	Consistency	333 ms	No diff.	999 ms	No diff.	–	
	Accuracy		No diff.		No diff.		
Duchek et al. (1994)	Consistency	–		550 ms	No dif.	–	
	Accuracy			550 ms	No diff.		
Krampe et al. (2005)	Consistency	300 ms	No diff.	400 ms/600 ms/800 ms/1,000 ms	No diff.	1,200 ms/1,600 ms/2,000 ms	No diff.
	Accuracy		No diff.		No diff.		No diff.
Krampe et al. (2010):	Consistency	–		550 ms	No diff.	2,100 ms	No diff.
Single-task condition	Accuracy				No diff.		No diff.
Dual-task condition	Consistency				O<Y***		O<Y*
	Accuracy				O<Y*		O<Y**
McAuley et al. (2006)	Consistency	150 ms/225 ms/337 ms	No diff.	506 ms/759 ms	No diff.	1,139 ms/1,709 ms	No diff.
	Accuracy		No diff.		No diff.		O>Y
Nagasaki et al. (1988)	Consistency	200 ms/250 ms/333 ms	O<Y*	500 ms/1,000 ms	O<Y*	–	
	Accuracy		No diff.		No diff.		
Thompson et al. (2015)	Consistency	–		500 ms/667 ms	O<Y***	–	
	Accuracy				O<Y*		
Turgeon et al. (2011)	Consistency	–		600 ms/900 ms	No diff.	–	
	Accuracy				No diff.		
Vanneste et al. (2001)	Consistency	300 ms	No diff.	400 ms/500 ms/600 ms/700 ms	No diff.	–	
	Accuracy		No diff.		No diff.		

*For simplification, paradigms using synchronization with continuation and synchronization–continuation are reported together here. O, old participants; Y, young participants; IOI, inter-onset interval. *p<0.05; **p<0.01; ***p<0.001.*

as fast as possible, older people tapped at a slower rate than younger people (Nagasaki et al., 1988; Cousins et al., 1998; McAuley et al., 2006; Turgeon et al., 2011). This fastest tempo may slow down most evidently from the age of about 70 years onwards (McAuley et al., 2006). Conversely, McAuley et al. (2006) also made their participants tap as slowly as possible at a constant rate, in which case older people sped up more than younger people. It appears, then, that aged people have a narrower range of tempi at which they can consistently produce taps than young people.

The variability of taps at a fastest regular speed has not always been investigated. Where it has, CV was shown to be affected by aging, although this effect was weaker than the effect of aging on interval size. More specifically, Turgeon et al. (2011) found age to account for 7% of the variance in CV scores and for 32% of the variance in ITI, which might reflect decreased attention in old age.

Paced Tapping

Synchronization Without Continuation

In tasks requiring participants to synchronize their tapping with an external regular signal, differences between young and old have been less clear than in the unpaced tapping tasks described above (see **Table 2**). First of all, several studies did not find differences between these two groups in terms of variabilities or accuracies (Krampe et al., 2005; Drewing et al., 2006; Turgeon et al., 2011). Contrary to that, Nagasaki et al. (1988) did find CV to correlate with age at all the intervals examined (between 200 and 1,000 ms), but did not find a significant effect of age on asynchronies.

One study (Thompson et al., 2015) did report differences between old and young participants in both variabilities and accuracies. In this study, older adults (age range 51–80) tapped to a regular beat with a higher variability and with a larger asynchrony than younger and middle-aged adults (age range 18–43). These results may seem surprising, especially in light of the relatively young age of their old adults group ($M_{\text{Age}} = 63.67$; for comparison, Drewing et al., 2006 did not find such age-related effects in the group of people aged 78–88). However, the difference found by Thompson et al. (2015) may, at least in part, be explained by musical experience. Since the authors were interested in how musical experience influenced beat synchronization, they recruited many musically experienced participants (in the young and middle-aged adult groups, there were 32 people with and 11 people without musical background). However, musical background was not assessed in the group of older adults, and therefore old and young adults may have not been matched on this variable. In fact, the respective asynchronies found in this study (around 40 ms before the beat for the older group and around 15 ms before the beat for the younger groups) are remarkably close to values that have previously been found in research comparing musicians and non-musicians (Aschersleben, 2002). Assessing musical training in all groups, including older adults, would have made it possible to verify whether young and middle-aged adults' superior performance was due to musical experience rather than age, and also to investigate whether musical training could be a neuroprotective factor in aged people.

Up until now, all studies we discussed here described paradigms in which people synchronized their movements to an isochronous sequence of repeating single beats. And in fact, while a large part of those studies discussed their results in terms of their relevance for music perception and cognition, one could argue that their stimuli were not strictly musical. People move spontaneously to a musical beat (Leman et al., 2017), even though this beat is a perceptual construct that does not have a clear physical correlate. Beats sometimes co-occur with musical notes, but not necessarily: A beat can occur on a silent event (McAuley, 2010). Extracting a beat from a complex auditory signal, such as music, while automatic, might be a quite different process than merely synchronizing to an explicit beat. And therefore, this process might be differently affected by aging and NCDs. Indeed, rhythm difficulties might be more easily identified with music than with simple, repeating tones (Sowiński and Dalla Bella, 2013; Falk et al., 2015). Another reason to look at music in addition to metronomic sequences is that generally, people tend to tap with a higher asynchrony (that is, their taps precede the corresponding stimulus onset) when synchronizing with a metronome compared to music (Thaut et al., 1997; Aschersleben, 2002), a result that has recently been confirmed in elderly people (Ghilain et al., 2020a,b), but still lacks a definitive explanation. It has been suggested that subdivision of intervals between beats leads to a reduction of negative asynchronies and their variability, and that synchronization may be facilitated by the recurrence of different pitches, event duration, or intensities (Repp, 2003). In this way, music could be seen as an extreme case of subdivision, and the observed pattern of reduced asynchronies in tapping to music might be no different from what has been observed in tapping to a subdivided metronomic sequence. In either case, however, no studies exist to the best of our knowledge that compare old and young participants on an SMS task requiring participants to tap along with an auditory complex, that is, musical, stimulus.

Synchronization–Continuation

In synchronization–continuation tasks, participants first synchronize with a metronome and then continue tapping at the same rate when the sound has stopped. Generally, only the performance in the continuation phase is analyzed (Wing and Kristofferson, 1973). Regarding the question of how older adults perform in this paradigm, the results are somewhat mixed (see **Table 2**). Turgeon et al. (2011) used a synchronization–continuation paradigm in which the target tempi per individual were determined based on one's SMT in the preceding spontaneous tapping task (see Section "Spontaneous Motor Tempo"). At the intervals IOI = 600 ms and IOI = 900 ms, age did not significantly predict variability or accuracy.

Other studies also did not find any differences in ITI or variability on synchronization–continuation tasks using tempi between 300 and 700 ms (Duchek et al., 1994; Vanneste et al., 2001). One study found intact performance in old subjects even at intervals as short as 150 and 225 ms (McAuley et al., 2006), but a higher asynchrony (speeding up) at the slowest target interval (1,709 ms) in their oldest group (75 years and above), but not in the group of 60–74-year-olds. Conversely, Carment et al. (2018) reported an increase in variability among older subjects at the IOI of 333 ms, but not at 500 and 1,000 ms. Another study found differences in both variability and accuracy among older participants at a target interval of 1,500 ms, but not at 500 ms or 1,000 ms (Bangert and Balota, 2012). These results lend support to the purported existence of two systems involved in temporal perception, an automatic and a cognitively controlled one, the latter of which is particularly implicated in the processing of slow intervals and presumably used less efficiently by older people.

Krampe et al. (2010) conducted a study with a dual-task design in which participants were required to tap to a faster (IOI = 550 ms) or slower (IOI = 2,100) tempo, while performing variants of the NBack WM task (Dobbs and Rule, 1989). In this task, participants were exposed to a sequence of visual stimuli and were asked to indicate when the current stimulus matched the one presented two steps earlier in the sequence. While this paradigm falls a bit outside the order of simple synchronization–continuation paradigms presented here, it is relevant for two reasons. First, the authors also report performance under single-task conditions, that is, while performing synchronization–continuation without a concurrent second task. In this case, there was no difference in variability or accuracy among age groups, even at the slow tempo of IOI = 2,100 ms, which is in contrast to the speeding up among oldest subjects in study of McAuley et al. (2006) study and the lower consistency and accuracy observed in oldest participants of Bangert and Balota (2012). This discrepancy might in part be explained by age differences: While older participants of Krampe et al. (2010) had a M_{Age} of 67, healthy old participants of Bangert and Balota (2012) were on average 75 years old and McAuley et al. (2006) included only people aged 75 or older in their oldest group. Therefore, it indeed appears to be difficult at least for very old people to synchronize successfully with a fading stimulus presented at a slow tempo (of at least an IOI = 1,200 or more).

The second reason for which study of Krampe et al. (2010) study is relevant to this review is that the dual-task nature of the paradigm might provide relevant information regarding the cognitive mechanisms involved in tapping at slow frequencies. Dual-tasking caused people regardless of age to speed up at the slow tempo, but additionally caused old participants to speed up at the fast tempo. Similarly, variability was significantly higher in older adults (at fast and slow tempi), but only in the dual-task condition. The authors' interpretation is that maintaining temporal precision and stability, even at a tempo of IOI = 550 ms, might be a quite automatic process in younger people, but might cost older people more attention and WM resources, in line with the compensation hypotheses mentioned above. Without any cognitive load, they can deploy that attention and WM resources to perform the task as well as their young counterparts. However, with fewer of these resources available,

TABLE 3 | Studies investigating spontaneous motor tempo and spontaneous tapping in people with and without neurocognitive disorders.

Study		Healthy	Mild NCD	Major NCD
Ghilain et al. (2020a)	SMT in ms (SD)		Between-group difference in SMT: n.s.	
	Consistency		Between-group difference in CV: n.s.	
Martin et al. (2017)	SMT in ms (SD)	820.33 (237.68)	_	935.88 (381.72)
	Consistency		*Not computed*	
Rabinowitz and Lavner (2014)	SMT in ms (SD)	581***	747***	
	Consistency		*Not computed*	
Roalf et al. (2018)	*n*	131	46	62
	SMT in ms (SD)	438*[a] (67)	468*[a] (102)	468*[a] (91)
	Consistency (IIV)	0.72*[a]	0.83*[a]	0.82*[a]

NCD, neurocognitive disorder; SMT, spontaneous motor tempo; SD, standard deviation; IIV, intra-individual variability; CV, coefficient of variation; n.s., not significant. [a]*Major and mild NCD groups significantly different than healthy group; no difference between major and mild NCD.*
$*p<0.05$; $***p<0.001$.

their performance will drop. Indeed, as we discussed in Section "Brain and Cognitive Correlates of Healthy Aging and Neurocognitive Disorders," it may be the cumulative effect of slow tempo, cognitive load, and age-related competition for prefrontal resources due to compensatory rewiring of the motor system that is expressed in the lower performance of older people.

Conclusion: Sensorimotor Synchronization in Healthy Aging

Perhaps the clearest finding regarding aging and SMS is a lower SMT in older people, which has been demonstrated in people in their 60 s and above but may be most apparent from the age of around 75 years onward. Similarly, preferred perceptual tempo appears to slow with age and to correlate with SMT. In contrast, variability appears to be intact in old participants tapping at a self-chosen speed. Moreover, the range of rates at which aged participants can tap regularly is narrower than for young participants, with a slower fastest tempo and a faster slowest tempo.

Paced tapping tasks have not tended to reveal differences in variability or accuracy between old and young subjects. Exceptions are synchronization–continuation tasks where participants had to maintain a relatively slow rate beyond 1 s, in which older people tended to speed up and tap less consistently, especially very old people from around 75 years old. Higher variability has also been reported at fast intervals of 333 ms and below and some research points to an interaction between age and cognitive load even at intervals that are close to people's natural pace.

SENSORIMOTOR SYNCHRONIZATION IN NEUROCOGNITIVE DISORDERS

Unpaced Tapping

Spontaneous Motor Tempo

Having discussed the relative slowing of SMT with age, we now discuss how this variable is affected by NCD. A few sources have suggested that unpaced tapping may become more variable and SMT may slow in NCDs, especially in advanced stages (see **Table 3**). Roalf et al. (2018) found people with AD and MCI to tap with a higher variability compared to age-matched healthy controls, and variability was negatively associated with their score on the Mini-Mental State Examination (MMSE; Folstein et al., 1983), a widely used test for screening cognitive function among the elderly. People with AD produced significantly fewer taps during 1 min of tapping at a comfortable rate compared to healthy participants, whereas the speed of participants with MCI did not significantly differ from either of the other groups. The difference in produced ITI between the AD group and healthy older adults was significant, albeit not very large (469 and 441 ms, respectively). Similarly, Rabinowitz and Lavner (2014) found that in a group composed of patients with MCI and patients with a diagnosis of dementia, variability was higher in that group than in healthy controls. Moreover, patients tapped at a slower speed (747 ms) than their healthy counterparts (581 ms). Additionally, MMSE score was found to be correlated with mean ITI, suggesting a slowing of SMT with disease progression. In contrast, some other studies compared people with and without NCD on a spontaneous motor tapping task and did not find any differences in ITI or variability (Martin et al., 2017; Ghilain et al., 2020a). In these studies, subjects tapped at a comfortable speed for 30 s or for 30 ITIs, respectively. The apparent disagreement in the literature may be explained by different instructions that were given. The durations in which people performed the SMT task were shorter in Roalf et al. (2018; six blocks of 10 s) and Rabinowitz and Lavner (2014; one block of 15 s). In just 10 or 15 s, even when told to tap at a comfortable speed, people might feel pressure to produce as many taps as possible. Indeed, the produced ITIs were relatively low, even compared to the ITIs found in the studies on SMT in healthy aging (see **Table 1**). Although speculative, it may be that people with NCD react to this pressure differently than healthy older adults. Additionally, cognitively impaired people might potentially have had more problems understanding the task instructions. If, due to lack of clarity of the task requirements, people with NCD tapped more hesitantly (slower and more variably) in the beginning of a task, this would be reflected in their overall scores more heavily if the whole trial was just 10 or 15 s long.

Therefore, the SMT tasks used in Ghilain et al. (2020a) and Martin et al. (2017), affording their participants more time to establish a regular tapping pattern reflective of their internal speed, might be a better representation of their real SMT. Indeed, the rates observed in their studies, which lay roughly between 700 and 950 ms, are close to SMT values that have been observed in physiological aging (see **Table 1**). It therefore does not appear that during spontaneous tapping, ITI and consistency deteriorate in NCD, at least not in the mild to moderate stages of NCD that participants in all the studies quoted above tended to be in. More research, particularly including people with more severe NCD, is needed to establish an effect or absence of effect of NCD on SMT.

Fastest Unpaced Tapping

As with healthy aging, some studies have looked into the variability and speed at which people with major and mild NCD tap when asked to tap regularly as fast as possible.

Under these conditions, Kluger et al. (1997) identified no difference in terms of produced tempo between patients with MCI and age-matched healthy participants, but found people with mild AD to tap at a lower speed. In contrast, Goldman et al. (1999) did not find an effect of AD on produced fastest tempo. Variability was not taken into account in these studies. Colella et al. (2021) did find tapping variability to increase in people with MCI, but they did not find a difference in tempo between the groups. Taken together, these studies suggest that while a decrease in fastest tempo at which people can tap is only seen in advanced stages of NCD, regularity of fast tapping already appears to decrease in people with mild NCD. This is an interesting parallel to the results found by Roalf et al. (2018), who also observed decreased variability in people with MCI but decreased absolute tempo only with a diagnosis of AD in their SMT task.

To the best of our knowledge, there do not exist any studies comparing people with and without NCD on the ability to tap in a regular fashion as slowly as possible. Since paced tapping at a slow tempo might rely more heavily on WM and attention, we might infer that people with NCD, who tend to be impaired in these domains, might speed up and/or tap with a higher variability when instructed to keep a regular pace as slowly as possible, a prediction that remains to be tested.

Paced Tapping

Synchronization Without Continuation

The performance of tapping along with an auditory metronome has been investigated in people with NCDs in few studies. There might be several reasons for this, but we presume that many of the tasks described in the last few sections could not have been conducted in the same fashion with people with NCDs, especially in groups of patients with major NCD. In this group, particular attention must be paid to avoid stressful, unpleasant, artificial, and invasive laboratory situations. The listening and movement production tasks described in the previous sections might not be suitable for this patient group, and instead research with multimodal stimuli that creates a social or quasi-social situation might be conducive here (Desmet et al., 2017; Lesaffre et al., 2017). An example of this is the paradigm we described in Ghilain et al. (2020a,b), and Hobeika et al. (2021) in which participants were instructed to tap along with music or a regular metronome (IOI = 800 ms) while a musician, either seated across from the participant or projected onto a life-sized screen, vocalized and tapped along with the same stimulus. Under these conditions, benefitting from the presence of a musician, no differences in asynchrony or variability were found between people with and without NCD (see **Table 4**). It must be mentioned that the patients in this study were recruited from a day hospital rather than an inpatient care facility, so they might reflect a relatively independent and mildly impaired NCD group. Their average MMSE score of 20 was just on the fringe between mild and moderate cognitive impairment (Folstein et al., 1983), so we cannot exclude the possibility that a sample of more heavily cognitively impaired patients would show deficits in tapping performance compared to healthy older adults. The lack of effect of NCD might also be explained by other methodological variables, such as the use of only one tempo (close to elderly people's SMT, see **Table 1**) or the impact of social entrainment related to the presence of a partner during the task. Since this paradigm is adapted to people with major NCD, it would be interesting to have a group of more cognitively impaired people perform this task.

Besides this, there do not exist many studies evaluating SMS with complex auditory (musical) stimuli, although, as we argued in Section "Synchronization Without Continuation," it is not only interesting to directly compare SMS to metronomic sequences and SMS to music, due to the presumably different mechanisms involved in beat extraction, but providing musical stimuli can also be of particular value in creating an experimental situation that will make people with NCDs feel comfortable and that has some ecological validity.

One study that did uncover NCD-related differences in SMS was that by Henley et al. (2014). In this study, participants with different variants of frontotemporal dementia and AD synchronized with a metronome at an IOI of 1,500 ms. This study did not find differences in accuracy but higher variability in participants with behavioral variant frontotemporal dementia, but not in participants with other variants of frontotemporal dementia or AD, compared to healthy age-matched adults.

Synchronization–Continuation

Bangert and Balota (2012), whose study was mentioned in Section "Synchronization–Continuation" about healthy aging, had their participants tap at a rate of 500, 1,000, and 1,500 ms, after the metronome stopped. Besides comparing the performance of young and healthy old participants, they also compared the latter group's performance to that of people with very mild (mean MMSE = 27) and mild dementia (mean MMSE = 24). At the interval of 500 ms, they identified no group differences in terms of variability or accuracy (see **Table 4**). At 1,000 ms, people with dementia tapped with a greater variability but at the same accuracy as their healthy counterparts, whereas at 1,500 ms both consistency and accuracy were reduced in

TABLE 4 | Studies investigating paced tapping in people with and without neurocognitive disorders.

Study		Fast tempo (<350 ms)		Comfortable tempo		Slow tempo (>1,000 ms)	
		IOI	**NCD effect**	**IOI**	**NCD effect**	**IOI**	**NCD effect**
Bangert and Balota (2012)	Consistency		–	500 ms/1,000 ms	NCD < healthy**[b]	1,500 ms	NCD < healthy*
	Accuracy				No diff.		NCD < healthy**
Carment et al. (2018)	Consistency	333 ms	NCD < healthy***	500 ms/1,000 ms	No diff.		–
	Accuracy		No diff.		No diff.		
Duchek et al. (1994)	Consistency		–	550 ms	No diff.		–
	Accuracy				No diff.		
Ghilain et al. (2020a)	Consistency		–	800 ms	No diff.		–
	Accuracy				No diff.		
Henley et al. (2014) synchronization without continuation	Consistency		–			1,500 ms	NCD < healthy*[a]
	Accuracy						No diff.
Synchronization–continuation	Consistency						NCD < healthy*
	Accuracy						NCD < healthy*[a]
Martin et al. (2017)	Consistency		–	*Determined by SMT task*	NCD < healthy*		–
	Accuracy				No diff.		
Nichelli et al. (1993)	Consistency		–	1,000 ms	NCD < healthy***		–
	Accuracy				Healthy < NCD*[c]		

For simplification, paradigms using synchronization without continuation and synchronization–continuation are reported together here. IOI, inter-onset interval; NCD, neurocognitive disorders; SMT, spontaneous motor tempo.

[a] *Behavioral variant frontotemporal dementia, but not Alzheimer's disease (AD).*

[b] *At 1,000 ms, but not at 500 ms.*

[c] *AD patients were slower than elderly controls, but since elderly controls tended to underestimate the target interval, AD patients' responses were actually more accurate.*

**p < 0.05; **p < 0.01; ***p < 0.001.*

cognitively impaired people. These effects were stronger in people with mild compared to very mild dementia. Complementing these findings, Carment et al. (2018) found unimpaired performance with MCI and AD (mean MMSE = 22) at tapping rates of 500 ms and 1,000 ms, but increased variability at the most rapid tempo of 333 ms. Duchek et al. (1994) employed an IOI of 550 ms and found merely a non-significant trend toward higher variability. Nichelli et al. (1993) did not test their participants at shorter intervals, but found AD patients' variability to be larger than healthy participants' at an interval of 1,000 ms, corroborating findings of Bangert and Balota (2012). Along similar lines, Henley et al. (2014), in a synchronization–continuation task at 1,500 ms, found lower accuracy (speeding up) and greater variability in people with behavioral variant frontotemporal dementia, and greater variability in people with AD compared to healthy participants. Based on these studies, it appears that ITI and/or variability in people with NCD are only impacted at relatively long or relatively short intervals, presumably due to an impacted cognitively controlled timing system. However, it is important to point out that the participants in all these studies had on average very mild or mild NCDs.

In contrast, the patients in the study by Martin et al. (2017) tapped with a higher variability than healthy controls, even at a comfortable rate (in this study, the synchronization–continuation task was performed at a rate that depended on their SMT in the preceding spontaneous tapping task; see Section "Spontaneous Motor Tempo"). The apparent discrepancy between this study and the ones mentioned before might be explained by degree of impairment: The patients in study of Martin et al. (2017) had an average MMSE of 19, which indicates moderate cognitive impairment and which was lower than the MMSE scores reported in any of the studies mentioned above. Taken together, these results suggest that SMS performance in people with mild NCD might decline only at relatively long or short tempi, whereas in more severe cognitive impairment, people might tap less precisely even at tempi that are close to their natural speed. Nonetheless, more research about timing abilities in people with moderate or even severe cognitive impairment is needed.

Conclusion: Sensorimotor Synchronization in Neurocognitive Disorders

Overall, there is not a lot of evidence suggesting that tapping at a comfortable rate reveals differences between people with and without NCD. On the other hand, tasks requiring regular tapping as fast as possible have demonstrated increased variability even for people with mild NCD and increased variability as well as slower tapping in people with major NCD. The fact that changes in variability during unpaced tapping are visible even in people with mild NCD are relevant in terms of using motor tasks as a diagnostic tool: While motor speed might only reliably identify people with major NCD, tapping variability could be used to identify people who are at a risk for developing a more serious impairment. Indeed, in MCI, motor impairments are predictive of developing AD (Aggarwal et al., 2006; Ghilain et al., 2020a).

Presently, there is little research studying the effect of cognitive impairment on performance in simple tapping (synchronization without continuation) tasks, but the extant literature suggests that people with frontotemporal NCD might tap less precisely than AD patients and healthy controls at a tempo of 1,500 ms. More research is needed with more different tempi and different levels of cognitive impairment. More commonly, synchronization–continuation studies have been used, and suggested that people with NCD might speed up and show increased variability at slow IOIs from around 1,000 ms, as well as show increased variability at short IOIs below 500 ms. There is some suggestive evidence that even at a comfortable rate, people with a moderate or severe NCD might tap less precisely. Etiology of the NCD may play a role, with a possible interaction between tempo and type of NCD, but more research is needed with various groups of patients with NCD due to different causes, and different levels of impairment.

In short, there is a need for more research investigating SMS abilities in people with moderate and severe cases of NCD. At the same time, however, designing tasks adapted to people with NCD is not trivial: a great deal of effort has to be done to ensure people understand the instructions and to create experimental paradigms that are not stressful, invasive, or unpleasant to the participants. With the existing research, differences between people with and without NCD must be evaluated critically: It is important to verify that they tap into the mechanisms a study claims to test, or whether observed differences may reflect differences in motivation, comfort, or having well understood the instructions. Finally, a fruitful avenue of research would be more studies using musical stimuli of different levels of rhythmic complexity, not only to test the ability to infer and maintain an implicit beat, but also to create a situation that is engaging and motivating, ideally involving a social or quasi-social element resembling real-life musical interaction (Desmet et al., 2017; Lesaffre et al., 2017; Ghilain et al., 2020a,b; Hobeika et al., 2021).

FUTURE DIRECTIONS

To move forward, we suggest the following methodological considerations when conducting research about SMS abilities in healthy aging and NCDs. First, it is useful to employ designs that compare healthy young, healthy old, and cognitively impaired old participants in the same study, in order to disentangle effects of age and of neurodegenerative disorder. A few studies discussed here have done that (Bangert and Balota, 2012; Carment et al., 2018), but most have not. Second, the literature reviewed here suggests that age effects on SMS abilities may not be linear, so it is particularly important to include sufficient amounts of participants from the latest decades of life. Third, likewise, with regard to NCDs, etiology (AD, vascular NCD, frontotemporal NCD, etc.) and severity seem to play important roles when investigating their effects on SMS. We are aware of only one study that compared people with different types of NCDs (Henley et al., 2014). In terms of severity, it is valuable to compare people with major and mild NCDs, or to define neurocognitive impairment as a continuous variable, measured by rating scales, such as the MMSE, mentioned above, the Montreal Cognitive Assessment (Nasreddine et al., 2005), or the Mattis Dementia Rating Scale (Mattis, 1976). These scales need not be mutually exclusive but can be complementary instruments of evaluation of cognitive state (Freidl et al., 1996; Cullen et al., 2007; Arevalo-Rodriguez et al., 2013). Fourth, when conducting research with people with NCDs, particular attention should be paid to creating a pleasant and stimulating atmosphere and to avoid stress. Otherwise, it cannot be excluded that observed between-group differences are reflective of differences in motivation, discomfort, or comprehension of the instructions, rather than sensorimotor abilities. Finally, musical training should always be probed, to ensure that different participant groups are matched on this variable but also to test the possible rehabilitative or neuroprotective effect of music engagement in old age and NCD.

As we mentioned, it will be interesting to conduct more studies on SMS to music. SMS is about predicting, extracting, and maintaining a representation of a beat; however, this beat is not a physical entity but a cognitive percept that needs to be extracted, a process that might be quite different for real music than for isochronous metronomic stimuli. The question of whether aged people and/or people with NCDs have a particular difficulty or a particular ease synchronizing with a musical rhythm is at present still an open one.

Furthermore, this review discussed tasks in which participants produced rhythmic responses, but there also exists task assessing beat perception in a purely perceptual fashion, such as the Harvard Beat Alignment Test (Fujii and Schlaug, 2013) and some subtests of the BAASTA (Dalla Bella et al., 2017b). Moreover, rhythm production and perception can independently be impacted (Bégel et al., 2017). It would be interesting to test rhythm perception abilities specifically in elderly people with and without NCDs.

Since the focus of this review was SMS to simple isochronous or musical rhythms, we did not touch upon the topic of error correction. Although error correction is an ever-present process in SMS without which one would eventually become out of sync (Vorberg and Wing, 1996), it is usually examined by introducing perturbations of the IOI and testing how quickly and efficiently participants adapt their own tempo to them. Generally, a difference is made between phase correction and period correction, The former refers to an automatic, often unconscious mechanism of adaptation to subtle perturbations that is associated with primary and secondary somatosensory cortical activity, whereas the latter refers to a mechanism correcting for more obvious changes in the temporal sequence that depends on attention and awareness and involves brain networks, such as the basal ganglia, prefrontal, medial frontal, and parietal regions (Thaut et al., 1998; Repp, 2001; Praamstra et al., 2003; Repp and Su, 2013; Ross et al., 2018). It is conceivable that phase and period correction would be differently influenced by aging and NCDs. A study (Repp and Keller, 2004) that manipulated attention by introducing a concurrent mentally taxing task found period correction to be affected by this reduction in available attentional resources, whereas period correction was not. Furthermore, in a recent study with musicians (Versaci and Laje, 2021), attention was guided in a more explicit way by directing some participants' attention to temporal features of the task, in turn yielding higher accuracy and more efficient resynchronization after a perturbation of a relatively large size, probably employing period correction mechanisms. It can be conjectured that very old and old people would be especially impaired in tapping along with sequences containing tempo changes, particularly those large enough to depend on period correction mechanisms, and, in cerebral terms, on frontal and parietal integrity.

GENERAL CONCLUSION

Neurocognitive disorders, as well as healthy aging, are often associated with a decline in memory, attention, and executive function. Less often, we tend to think of sensorimotor dysfunction as a prototypical symptom of physiological and pathological aging, except in the case of Parkinson's disease. Restricting our review to the other etiologies of NCDs, we have indeed observed many examples in this review in which no clear difference on SMS performance emerged between young, healthy old, and/or cognitively impaired old people. However, SMS abilities are a complex set of skills with different subcomponents that may be differently affected by aging and NCDs, and substantial heterogeneity exists between and within different NCDs, as well as between aging brains in general.

In some cases, there is clear evidence for decline on SMS tasks for elderly people and/or people with NCDs. Specifically, SMS ability might be especially impaired above the age of around 75 and for people with moderate and/or severe NCDs. People with frontotemporal NCDs might particularly struggle with SMS tasks, although research comparing different NCD etiologies is sparse. These effects might be augmented with stimuli whose tempo is further away from a person's comfortable, natural tempo (i.e., IOIs faster than around 300 ms and slower than around 1,000 ms). The exact instructions, protocol, and trial length might play a role, especially in spontaneous motor tasks. Musical background might also modulate the effect of aging and NCDs on SMS abilities, and cognitive load might have a different effect on performance for the different groups. More specifically, due to rewiring and compensation mechanisms, SMS, usually a quite spontaneous process requiring little cognitive resources, might become heavier in cognitive load and interfere with other concurrent tasks. Rhythmic complexity might be relevant although our analysis was restricted to two ends of the extreme: simple, isochronous rhythms, and music, the latter of which merits more attention than it is currently given. To fully understand late-life development of sensorimotor processes, more research is needed that reflects the wide array of types of auditory stimuli as well as the diversity of aging brains.

The observation that slightly younger elderly people and people with mild NCDs tend to be relatively unimpaired in synchronizing particularly at tempi of around 500 and 1,000 ms is a strong argument for the use of music-based interventions. Musical tempi tend to lie within this range, and capitalizing on this relatively preserved skill could be a fruitful approach. The stimulation of motor systems in older adults across different levels of cognitive impairment may not only improve their sense of rhythm, but lead to emotional and cognitive benefits as well as improvements in the ability to predict the unfolding of events in the environment, leading to improved communication and reduced social isolation.

AUTHOR CONTRIBUTIONS

AS, LH, and SS: conceptualization. AS: writing the original draft. LH and SS: review, editing, and supervision. DH-G: review. All authors contributed to the article and approved the submitted version.

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Temporal Predictions in Space: Isochronous Rhythms Promote Forward Projections of the Body

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A regular rhythmic stimulation increases people's ability to anticipate future events in time and to move their body in space. Temporal concepts are usually prescribed to spatial locations through a past-behind and future-ahead mapping. In this study, we tested the hypothesis that a regular rhythmic stimulation could promote the forward-body (i.e., toward the future) projections in the peri-personal space. In a Visual Approach/Avoidance by the Self Task (VAAST), participants ($N = 24$) observed a visual scene on the screen (i.e., a music studio with a metronome in the middle). They were exposed to 3 s of auditory isochronous or non-isochronous rhythms, after which they were asked to make as quickly as possible a perceptual judgment on the visual scene (i.e., whether the metronome pendulum was pointing to the right or left). The responses could trigger a forward or backward visual flow, i.e., approaching or moving them away from the scene. Results showed a significant interaction between the rhythmic stimulation and the movement projections ($p < 0.001$): participants were faster for responses triggering forward-body projections (but not backward-body projections) after the exposure to isochronous (but not non-isochronous) rhythm. By highlighting the strong link between isochronous rhythms and forward-body projections, these findings support the idea that temporal predictions driven by a regular auditory stimulation are grounded in a perception-action system integrating temporal and spatial information.

Keywords: temporal prediction, isochronous rhythm, VAAST, body projection, embodied cognition

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INTRODUCTION

Music is a dynamic process occurring over time. During music listening, we constantly generate hypotheses about what could happen next in terms of time (i.e., *when* expectations) and content (i.e., *what* expectations; Tillmann et al., 2014). While *what* expectations are usually manipulated through changes in melodic or harmonic sequences (i.e., the spectral structure), *when* predictions are mainly related to the temporal structure of music, based on repeated beats (Koelsch et al., 2019). When exposed to isochronous rhythms (i.e., auditory stimulations with temporally equidistant beats), listeners are able to implicitly predict where each beat will fall in time (Cannon and Patel, 2021). At a behavioral level, temporal predictions driven by periodic stimulation have been shown to improve performance by increasing perceptual sensitivity and reducing response latencies (e.g., Jones et al., 2002; Stefanics et al., 2010; Lawrance et al., 2014; Morillon et al., 2016).

Human ability to perceive beat is closely related to movement on both behavioral and neural levels. People show a spontaneous tendency to move (from finger tapping to entire body movement) in response to the beat of rhythmic sound (Repp, 2005; Damm et al., 2020). In particular, successful motor synchronization seems to be driven by the more regular and predictable musical sequences (Dalla Bella et al., 2013). Furthermore, brain studies highlighted that mere listening to musical beat (i.e., in the absence of movement) can activate regions of the motor system (Zatorre et al., 2007; Grahn and Rowe, 2009). Even simple human actions such as walking are coordinated and rhythmic and have been shown to operate at a spontaneous preferred tempo of ∼1.5–2 Hz (see e.g., MacDougall and Moore, 2005; Zalta et al., 2020). Moving to the beat has been shown to benefit auditory perception tasks as well (Manning and Schutz, 2013; Morillon et al., 2014). In this case, the motor system, by simulating the rhythmic actions, might provide for temporal predictions about beat times in the auditory regions (Patel and Iversen, 2014; see also Gatti et al., 2021).

Taken together, these studies suggest that a regular rhythmic stimulation, by tapping on perceptual and motor processes, promotes people's body movement in space. A regular auditory stimulation is likely to stimulate people's ability to anticipate future auditory events in time. Indeed, according to the dynamic attending theory (Jones, 1976; Jones and Boltz, 1989; Large and Jones, 1999), the attentional resources are not distributed continuously and equally but cyclically develop over time. By entraining internal oscillations to an external regular rhythm, temporal regularities can then guide attention. Consequently, perceivers can develop predictions about the temporal occurrence of a future event and allocate more attentional resources at the expected moment, and this in turn results in enhanced cognitive processing of an event occurring at this moment (see e.g., Jones et al., 2002; Escoffier et al., 2010; Fanuel et al., 2018).

Such time–space link becomes particularly interesting within the embodied cognition framework (Glenberg, 1997; Wilson, 2002; Barsalou, 2008; Versace et al., 2014), which considers the abstract concept of time as embedded in a perception-action system and integrated with spatial information (Lakoff and Johnson, 1980; Núñez and Cooperrider, 2013). In daily life, we tend to prescribe temporal concepts to spatial locations through a past-behind and future-ahead mapping (e.g., we *move back to the past*, and *look forward to the future*; Boroditsky, 2000). Several studies highlighted that the ability to anticipate future events or mentally travel through the past is consistently related to physically moving in space forward or backward, respectively (i.e., a front-back representation; Torralbo et al., 2006; Miles et al., 2010; Rinaldi et al., 2016; Aksentijevic et al., 2019). For example, in a word categorization task, Rinaldi et al. (2016) showed that participants were faster to step forward in response to future-than past-related words, whereas they stepped backward faster in response to past-than to future-related words.

By showing a link between temporal processes and space-motor programming employing mental time traveling paradigms (i.e., related to remembering past events or thinking about the future; Tulving, 2002), these studies support the idea that cognition is dynamically rooted in the interactions that the body maintains with the environment over time (Barsalou, 2008; Bender and Beller, 2014; Versace et al., 2014). Although the tight coupling between the temporal qualities of music and movement is well stated in literature (see Levitin et al., 2018), to the very best of our knowledge, no study so far manipulated the predictability of a rhythmic stimulation to study the link between the abstract concept of time, spatial references frames, and body movements. Therefore, we aim here at investigating whether the ability to predict future events driven by a regular auditory stimulation can specifically influence movements in space through a backward–forward mapping.

To this aim, we employed an adapted version of the Visual Approach/Avoidance by the Self Task (VAAST, Rougier et al., 2018) to test participants' implicit forward and backward body movements following regular (i.e., isochronous) or irregular (non-isochronous) auditory rhythmic stimulations presented at different tempi. This task has been effectively used in previous studies to show the approach/avoidance compatibility effect (Solarz, 1960). Typically, participants provide faster responses to approach positive (vs. negative) stimuli and to avoid negative (vs. positive) stimuli presented in a virtual scene. Here, we used it to study whether the temporal regularity of auditory stimuli could impact the time taken to approach a visual scene or avoid it. We asked participants to make as quickly as possible a perceptual judgment on the visual scene (i.e., whether the metronome pendulum represented on the scene was pointing to the right or left). The responses could trigger a forward or backward visual flow, respectively approaching or moving them away (i.e., avoidance) from the scene.

We made the hypothesis that if temporal predictions promoted by a regular (but not irregular) rhythmic stimulations are grounded in a perception-action system integrating temporal and spatial information, and therefore are tightly related to forward body movements, then an isochronous rhythm should lead to faster responses associated to approach (i.e., forward) behavior than a less predictable, non-isochronous rhythms.

MATERIALS AND METHODS

Participants

Twenty-four non-musician participants (17f, mean age = 22.08, *SD* = 3.19), with normal or corrected-to-normal vision and reported normal audition were included in the study. Statistical sample size analysis run on G*power, based on an effect size of 0.25 and 95% confidence interval for the effect for a 2 × 2 × 2 within subject design (see Analysis section) indicated a total sample size of 23. All participants signed a written informed consent before the participation. The study was conducted in accordance with the Helsinki Declaration, seventh revision. Ethical review and approval were not required for the study on human participants in accordance with the local legislation and institutional requirements.

Auditory Stimuli

Auditory stimuli consisted of 3-s (enough to entrain synchronization, Trapp et al., 2020) isochronous and non-isochronous bass drum-like rhythmic tone sequences. To control whether an isochronous-effect over body movements could be generalized to different frequencies rather than being limited to preferred natural cadences (see Zalta et al., 2020), the auditory stimuli were presented at two different tempi, namely 120 (i.e., 2 Hz, similar to the preferred natural frequency) and 240 BPM (i.e., 4 Hz). In particular, for the isochronous rhythms (2 in total), the tone was regularly presented at a tempo of 120 or 240 BPM. The non-isochronous rhythms sequences (12 in total) consisted of the same tone presented for 6 or 12 subsequent pulsations with random intervals. The onsets of the first and the last tones remained constant across sequences (i.e., 0 and 3,000 ms, respectively; **Figure 1** and **Table 1**).

In order to control for possible affective responses associated to the auditory stimuli, participants' ratings of arousal and valence/pleasantness were collected after the main experimental task (see section below). After each auditory sequence, participants had to indicate, by moving a cursor on a bar on the screen (values ranging from 0 to 100), how much they rated the stimulus arousing (from very relaxing to very exciting) and enjoyable (i.e., valence, from lowly enjoyable to highly enjoyable).

Visual Approach/Avoidance by the Self-Task Task

The Visual Approach/Avoidance by the Self-Task (VAAST) developed by Rougier et al. (2018) relied on sensorimotor indices provided by a realistic visual flow on the screen stimulating whole-body movements in relation to an emotional stimulus (i.e., target words). In a series of six experiments, the authors showed that participants provided faster response times to approach (via a zoom-in on the screen approaching the subject to the scene) positive stimuli and avoid (via a zoom-out moving the subject away from the scene) negative stimuli, than the reverse (also known as the approach/avoidance compatibility effect, Solarz, 1960).

While the procedure originally investigated virtual body movements in relation to emotional stimuli, here we employed it to study whether the temporal regularity (or irregularity) of auditory stimuli could impact the time taken to produce a motor response generating forward (i.e., approaching) or backward (i.e., avoiding) visual flow. In our study, participants were seated in a comfortable chair in a soundproof experimental room and wore headphones. During a training phase, they were instructed to use with the index finger of the dominant hand three adjacent buttons disposed vertically on the keyboard (see **Figure 2**): a middle "start" button to start each trial, and two external buttons to perform the categorization task labeled "forward" (triggering the approach) and "backward" (triggering the avoidance).

The VAAST task consisted of 120 trials: 60 presented in the isochronous and 60 in the non-isochronous condition (i.e., 30 for the 120 BPM condition, and 30 for the 240 BPM one). The trials were divided into 5 blocks of 24 trials each (i.e., 6 trials for each experimental condition for each block). For each trial, a visual scene was presented on the screen. The visual scene represented a music studio with a metronome in the middle (see **Figure 2**). This scene was constructed in order to be realistic and coherent with the presented auditory stimulation. Participants were instructed to fixate a white circle placed in the middle of the screen, below the needle of the metronome. As soon as participants pressed the "start" button, the 3-s auditory stimulation (i.e., isochronous or non-isochronous, in a random order) started. During the auditory stimulation, the needle of the metronome was stationary. Immediately after, the needle of the pendulum in the middle of the visual scene randomly pointed to the left or to the right. Therefore, there was no pause between the end of the auditory stimulation and the moving needle on the screen. Participants were asked to indicate as fast and as correctly as possible whether the pendulum of the metronome was pointing to the right or left by pressing on the "forward" or "backward" button. The association between forward/backward

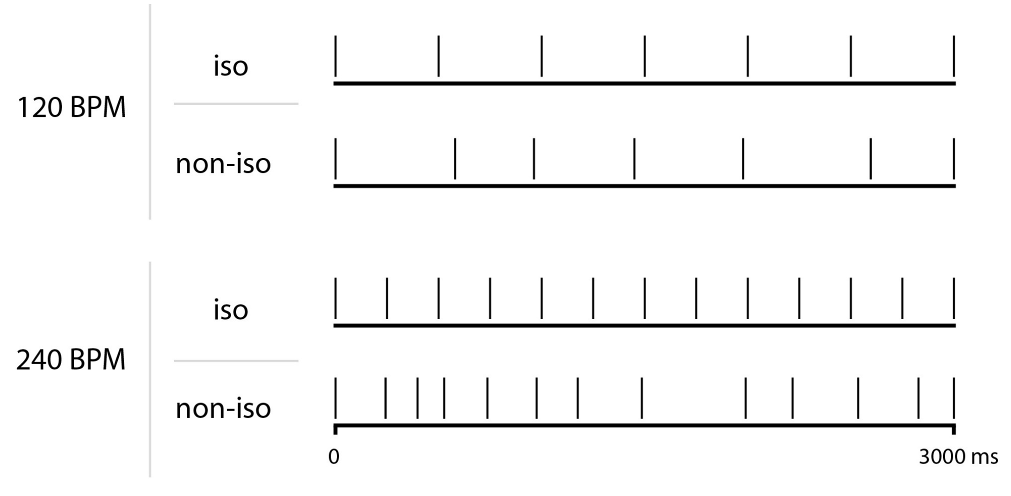

FIGURE 1 | Schematic representations of one isochronous (iso) and one non-isochronous (non-iso) auditory sequence, for each tempo (i.e., 120 and 240 BPM). Each vertical line represents a tone (see **Table 1** for a complete description).

button and left/right response was counterbalanced across participants. For correct responses, according to the participants' approach/avoidance action, the visual environment was zoomed in (i.e., approach, "forward" button) or zoomed out (i.e., avoidance, "backward" button) by 30% after each button press, thus giving the visual impression to move forward or backward as a consequence of these actions. After the zoom, the initial scene was reset on the screen for the next trial. The incorrect answers did not trigger any visual flow and were accompanied by a visual feedback of error (i.e., a red cross on black background).

Analysis

Reaction times (RTs) of correct responses to the perceptual categorization task were first computed for each participant. Outlier RT values (i.e., ±2.5 standard deviations from the mean) within each experimental condition, corresponding to the 5.49% of the data, have been excluded from the analyses. In order to test the results of the VAAST task, we run a repeated-measures ANOVA (JASP 0.11.1.0) with correct responses RTs as a dependent variable and body movement (approach vs. avoidance), rhythm (i.e., isochronous vs. non-isochronous) and tempo (i.e., 120 vs. 240 BMP) as within-subject factors. In an additional analysis, in order to test for an eventual congruency effect between left-right responses and past-future representations, we added the left/right counterbalancing (i.e., the association between forward/backward button and left/right response across participants) as between-subject factor.

In order to investigate possible difference in subjective ratings of auditory stimulation, we run repeated-measures ANOVAs with rhythm (i.e., isochronous vs. non-isochronous) and tempo (i.e., 120 vs. 240 BMP) as within-subject factors on both arousal and valence subjective ratings.

RESULTS

RTs analysis showed a good overall performance of participants, with the 94.51% of correct responses in the left-right categorization task. Repeated-measures ANOVA on VAAST task revealed an effect of body movement, indicating that participants were faster in providing responses associated to approach rather than avoidance movements [$F(1, 23) = 16.53$ $p < 0.001$, $\eta^2 = 0.135$; **Figure 3**]. A main effect of rhythm was also observed, with faster responses following isochronous than non-isochronous auditory stimulation [$F(1, 23) = 25.77$, $p < 0.001$, $\eta^2 = 0.145$], and independently from the tempo variations ($F < 1$). Crucially, results showed a significant interaction between body movements and rhythm [$F(1, 23) = 57.79$, $p < 0.001$, $\eta^2 = 0.114$], with participants providing faster approaching responses after isochronous than after non-isochronous auditory stimulations ($t = -8.139$, $p < 0.001$, Bonferroni-corrected), and without significant difference between rhythmic conditions in the avoidance body movement responses ($t = -0.49$, $p = 1.000$, Bonferroni-corrected). We found no significant effect of counterbalancing of forward/backward movement and right/left responses [$F(1, 22) = 1.71$, $p = 0.204$, $\eta^2 = 0.034$], nor any interactions involving this factor.

The repeated-measures ANOVAs on affective ratings did not show any significant effect of rhythm and tempo on arousal ($F < 1$ for both rhythm and tempo) nor valence subjective ratings

TABLE 1 | Description of onsets (in ms) in isochronous (iso) and non-isochronous (non-iso) tones sequences, for the 120 (a., i.e., a total of 7 tones) and 240 BPM tempi conditions (b., i.e., a total of 13 tones).

a. Tempo	120 BPM						
Tones sequence	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Iso	0	500	1000	1,500	2000	2500	3000
Non-iso1	0	676	997	1486	1988	2185	3000
Non-iso2	0	805	1244	2117	2309	2618	3000
Non-iso3	0	245	434	870	1622	2683	3000
Non-iso4	0	434	1185	2247	2686	2818	3000
Non-iso5	0	248	436	1945	2247	2813	3000
Non-iso6	0	186	997	1185	1624	1999	3000

b. Tempo	240 BPM												
Tones sequence	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**
Iso	0	250	500	750	1000	1250	1500	1750	2000	2250	2500	2750	3000
Non-iso1	0	246	374	502	746	997	1125	1499	1996	2248	2562	2867	300
Non-iso2	0	246	617	748	877	1182	1314	1439	1745	1999	2433	2564	3000
Non-iso3	0	249	500	625	997	1245	1497	1628	1999	2248	2496	2624	3000
Non-iso4	0	251	371	746	874	1000	1248	1497	1622	1996	2125	2253	3000
Non-iso5	0	235	374	746	997	1248	1376	1499	1622	2125	2250	2559	3000
Non-iso6	0	245	498	873	1000	1248	1498	1749	1873	2121	2248	2562	3000

The onsets of the first and the last tones remained constant across sequences.

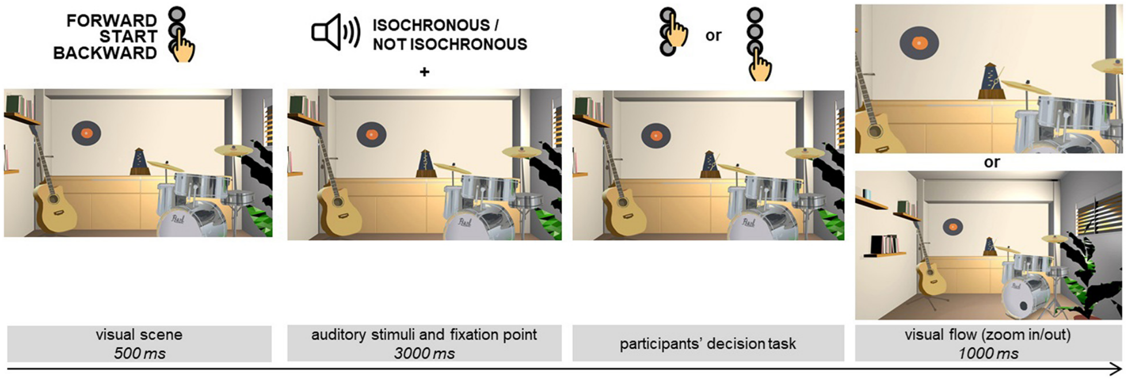

FIGURE 2 | Schematic representation of the experimental procedure.

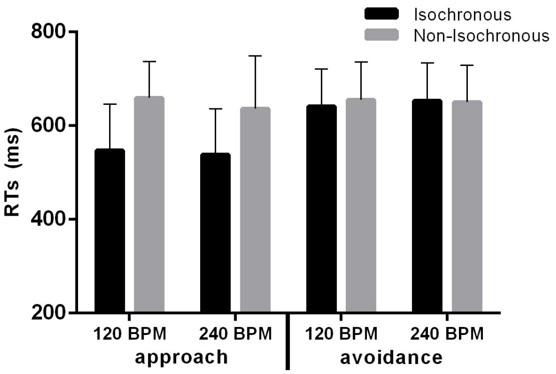

FIGURE 3 | Results of the VAAST task showing RTs for correct responses according to the body movement (approach/avoidance), auditory rhythmic stimulation (isochronous/non-isocrhonous) and tempo (120/240 BPM). Analysis revealed significant main effects of body movement and rhythm, as well as a significant interaction body movement × rhythm, thus indicating that participants were faster in approach (vs. avoidance) response following an isochronous (vs. non-isochronous) auditory stimulation.

[for rhythm, $F < 1$; for tempo, $F(1, 23) = 1.140$, $p = 0.297$; see **Table 2**].

DISCUSSION

In this study, we aimed at investigating whether a regular rhythmic auditory stimulation, by allowing anticipation in time, could promote forward body projections in the peri-personal space as compared to an irregular, non-isochronous rhythm. Using an approach/avoidance task in a visual virtual environment, we found that participants provided faster forward-approach (but not backward-avoidance) responses following an isochronous (but not non-isochronous) auditory stimulation. Importantly, temporal regularities promoted forward projections of body movements no matter the tempo of the auditory stimuli, thus suggesting a generalizable effect relying on the isochronous nature of the stimulation rather than on its preferred spontaneous frequency (MacDougall and Moore, 2005; Zalta et al., 2020).

TABLE 2 | Means and standard deviations (SD) of mean arousal and valence subjective ratings according to auditory stimulation (Iso, isochronous; Non-iso, non-isochronous) and tempo (120 and 240 bpm).

		Arousal		**Valence**	
		120 bpm	**240 bpm**	**120 bpm**	**240 bpm**
Iso	Mean	51.27	56.36	50.96	58.45
	SD	19.07	22.71	19.03	18.77
Non-iso	Mean	52.88	56.28	54.25	53.80
	SD	14.15	16.13	12.59	15.22

No significant differences were found across experimental conditions.

Research on temporal dynamics has shown that a constant duration of intervals delineating an isochronous (rhythmic) stimulation promotes an accurate prediction about when event is likely to occur, and therefore allows attention resources to be oriented toward that moment in time (Jones and Boltz, 1989; Large and Jones, 1999; Jones et al., 2002). Such temporal predictability of isochronous sequences has been shown to consistently improve sensorimotor processing of events occurring in phase with the rhythm, thus enhancing not only perceptual sensitivity (Morillon et al., 2014) and target detection speed (Bolger et al., 2014), but also working- (Fanuel et al., 2018, 2020; Plancher et al., 2018) and long-term memory (Thavabalasingam et al., 2016) processes. Here, we considered the tight time–space relationship, according to which temporal concepts are usually prescribed to spatial locations through a past-behind and future-ahead mapping (Lakoff and Johnson, 1980; Núñez and Cooperrider, 2013). As humans, we tend to conceptualize time along the sagittal space (Bender and Beller, 2014), thus representing the past as "back" and the future as "forward" (Núñez and Cooperrider, 2013). Accordingly, many studies have shown that motor responses to past- and future-related information are significantly faster when the response direction is compatible with such sagittal mental time line (Sell and Kaschak, 2011; Rinaldi et al., 2016, 2018; Walker et al., 2017). Our findings suggest that a close link exists between temporal dynamics triggered by regular rhythms and body projections in space over such sagittal representation.

In particular, by showing for the first time that regular auditory stimulations are related to forward, but not backward body movements, our results support the idea that cognition is rooted in the interactions between the body and the environment and projected onto a temporal dimension (see Barsalou, 2008; Versace et al., 2014). From a more speculative perspective, our findings would suggest that isochronous-related benefits on perception and cognition could be based on, or at least intrinsically related to the concept of projections in space. Indeed, temporal regularities might promote the sensorimotor anticipations in space likely to benefit perceptual and cognitive processes (Barsalou, 2008; Pezzulo, 2011; Koziol et al., 2012).

In order to provide an ecological, realistic, and immersive virtual environment likely to promote participants body projections in space, we decided to employ the VAAST task (Rougier et al., 2018; see also Cereghetti et al., 2021 for an adaptation in another sensory modality). However, it is worth mentioning that the nature of the paradigm itself could suggest possible alternative interpretations of results. First, the procedure originally relied on verbal emotional stimuli and showed that participants' responses were faster in approaching positive and avoiding negative stimuli (i.e., approach/avoidance compatibility effect, Solarz, 1960). In our study, we were interested in the impact of the temporal regularities on the time taken to produce a motor response generating a forward or backward visual flow. One might therefore argue that the faster responses following isochronous auditory stimulation are related to a more positive emotional valence associated with temporal regularities (vs. irregularities; Rougier et al., 2018). However, the affective (i.e., arousal and valence) subjective ratings provided by our participants did not show any significant difference between isochronous and non-isochronous auditory stimulations, thus excluding an approach/avoidance compatibility effect driven by hedonic-emotional responses.

Another possible interpretation of our findings relies on the fact that participants were asked to provide responses associated to approach/avoidance body movement toward the center of the screen, represented by a metronome. As the metronome is usually associated to regular rhythmic stimulation, faster approach responses following isochronous rhythms could reflect congruency effect. Further studies employing more neutral stimuli would help to disentangle the contribution of stimuli congruency in the observed findings. However and crucially, we showed that our participants were faster in approaching the metronome after an isochronous rhythm, but not in avoiding it after a non-isochronous auditory stimulation. Therefore, our results would point to a specific effect of isochronous-driven temporal prediction over body movements in space rather than a more general priming-congruency effect.

Such isochronous-driven facilitation over forward movements can also be explained by the fact that our daily body activities in space, such as walking or running, usually follow a regular rhythm and are associated with forward body movements. Many studies have shown the deep relationship between isochronous auditory sequences and ambulation. For example, convergent evidence has shown that regular beats are able to enhance perceptual and motor timings in Parkinson's patients, in turn improving their gait (e.g., Benoit et al., 2014; Dalla Bella et al., 2017; Koshimori and Thaut, 2018). However, in our study we observed no specific facilitation of preferred walking tempo (i.e., our 120 BPM condition; see MacDougall and Moore, 2005; Zalta et al., 2020) on participants' performance. Furthermore, the influence of time representation (i.e., backward-past, forward-future) on whole-body movements has been well documented (e.g., Rinaldi et al., 2016). It appears therefore difficult to disentangle the contribution of the motor (i.e., ambulation) and time representation (i.e., backward-past and forward-future) components in the observed findings. An interesting perspective would be to investigate, in future research, cultures in which the time representation is inverted, with a timeline representing past forward and future backward (Núñez and Sweetser, 2006; Boroditsky et al., 2011). If our results could be entirely explained by the motor-ambulation component, then this should act independently from the time–space representation, and we should observe in these cultures the same effect as the one observed in the present work. Otherwise, if the motor component works intertwined with time–space representation, then the isochronous facilitation over forward body movements should disappear or be significantly reduced.

In sum, this study shows for the first time that a tight link exists between isochronous auditory stimulations, likely to promote the anticipation of events in time, and forward-body projections in the peri-personal space. Taken together, our findings support the idea that temporal predictions driven by a regular auditory stimulation are grounded in a perception-action system integrating temporal and spatial information.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

Ethical review and approval were not required for the study on human participants in accordance with the local legislation and institutional requirements. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

LF, RV, and CV made substantial contributions to the conception and design of the work and the acquisition, analysis, and interpretation of data for the work. LF, RV, and GP drafted the work and revised it critically for important intellectual content. LF, RV, CV, and GP gave final approval of the version to be published and agreed to be accountable for all aspects of the work in ensuring that questions related to the accuracy and integrity of any part of the work are appropriately investigated and resolved. All authors contributed to the article and approved the submitted version.

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ORIGINAL RESEARCH
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Synchrony During Online Encounters Affects Social Affiliation and Theory of Mind but Not Empathy

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Moving together in time affects human social affiliation and cognition. However, it is unclear whether these effects hold for on-line video meetings and whether they extend to empathy (understanding or sharing others' emotions) and theory of mind (ToM; attribution of mental states to others). 126 young adult participants met through online video in unacquainted pairs. Participants either performed 3 min of synchronous arm movements paced by sounds ($n = 40$), asynchronous movements ($n = 46$) or a small talk condition ($n = 40$). In a subsequent empathy task, participants engaged in a conversation. A video recording of this conversation was played back, and each participant rated, at predetermined time points, how they felt and how they thought their partner felt. From this we calculated empathic accuracy (accuracy of the estimation of the other's emotions) and emotional congruence (emotion sharing). ToM was measured by showing videos of geometrical shapes interacting and asking the participants to describe what happened, measuring the amount of intentionality. We found that participants in the synchrony condition rated feeling greater closeness and similarity to their partners relative to the asynchronous condition. Further, participants in the synchrony group tended to ascribe more intentionality to the abstract shapes than participants in asynchrony condition, suggesting greater ToM. Synchrony and asynchrony groups did not reliably differ in empathic accuracy nor emotional congruence. These results suggest that moving in synchrony has effects on social affiliation measures even in online encounters. These effects extend to ToM tendencies but not empathic accuracy or emotion sharing. These results highlight the potential of synchronous movement in online encounters to affect a subset of social cognition and affiliation measures.

Keywords: synchrony, theory of mind, empathy, social affiliation, online meetings, closeness

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INTRODUCTION

People moving in synchrony occurs in cultures across the globe in activities ranging from rituals and ceremonies to military marching (McNeill, 1997). Synchronous movement appears early in life (Cirelli, 2018). Synchronization can occur spontaneously during an interaction or can be intentional as when ensemble musicians adjust their movements to each other (bidirectionally) or when orchestra members follow the beat imposed (unilaterally) by a conductor. Synchrony has a wide range of effects on human social cognition, promoting social bonding (Huron, 2001) and enhancing social cohesion (Hove and Risen, 2009; Wiltermuth and Heath, 2009) and cooperation (Wiltermuth and Heath, 2009) both within and outside behaviorally synchronous groups (Reddish et al., 2014; Sullivan et al., 2015) (but see also Gelfand et al., 2020). The aim of the present study was to investigate whether these effects hold for online encounters between unacquainted pairs of young adults and whether these effects extend to more complex socio-cognitive abilities such as theory of mind (e.g., ToM) and empathy.

Moving in synchrony with somebody, whether spontaneous or imposed, has previously been shown to increase the sense of connection and liking (Hove and Risen, 2009; Tarr et al., 2015, 2016) and boost individual perception of closeness and feelings of similarity (Paladino et al., 2010; Valdesolo et al., 2010; Vacharkulksemsuk and Fredrickson, 2012; Reddish et al., 2013; Tarr et al., 2016). Synchrony has also been shown to increase positive affect (Tschacher et al., 2014) and to improve memory recall of words spoken by the person that one synchronizes with (Macrae et al., 2008). Drawing on a meta-analysis including more than 4,000 participants, Mogan and colleagues concluded that moving in synchrony increases four main dimensions of social relationships: social behaviors, such as prosocial actions, social bonding, including the feeling of similarity and closeness, social cognition, such as the ability to memorize or paying attention to others, and positive affect, such as mood, happiness, self-esteem, and general life satisfaction (Mogan et al., 2017). Altogether these studies show that synchrony affects several dimensions of social affiliation such as closeness, prosocial behavior, and perceived similarity. Studies in this field have been typically conducted in person with participants being in the same room while performing the synchronous movements. Therefore, it is not clear whether synchrony can also affect social affiliation when participants meet online rather than in physical presence. This is not a trivial question as there are a number of key differences between online (video) and in-person meetings which may influence the social dynamics of these encounters (Day and Schneider, 2002). First of all, the fixed camera in online meetings forces people to stay relatively still in order to be visible hindering the regulation of social distance which is known to be an important part of natural conversation (Patterson, 1996). Second, in online encounters some sensory information is not shared between the interacting partners such as external sounds and odors, which can have an impact on perceived interaction and emotional engagement with the other person (Johnson et al., 2006; Sohn, 2011). These features may explain why it is more difficult to recreate a sense of 'being there together' in online encounters (Parkinson and Lea, 2011). Given the differences between online and in-person social interactions, we cannot assume that the effects of synchrony on social affiliation, which have been tested virtually exclusively in-person, generalize to online interactions. The first aim of the present study is to test whether, in online video meetings, synchrony affects social affiliation.

The second set of questions we address relates to socio-cognitive skills. Recently it was suggested that the effects of synchrony extend beyond social affiliation (e.g., closeness, social bonding) to also include people's socio-cognitive skills (Baimel, 2015). In particular, the present study focuses on the tendency to attribute mental states and intentionality to others, typically referred to as ToM, on the one hand, and on the accuracy of perceiving other's emotions and on the extent of sharing them, typically referred to as cognitive and affective empathy, respectively.

Connections between synchrony and empathy have been investigated, focusing predominantly on subjective reports. In one study participants rhythmically moved cups in time with sounds presented through headphones (Baimel et al., 2018). They did so in trios where either the sounds were synchronous (i.e., same tempo for all participants) or asynchronous (i.e., different tempi for different participants). As a result, participants performed movements at the same time in the synchrony but not in the asynchrony condition. Participants moving synchronously rated themselves as better in understanding others' emotions, but not in sharing these emotions, relative to participants moving asynchronously (Baimel et al., 2018). This latter result differs from Koehne et al. (2016) who tested participants in a unilateral synchrony task where participants, in a leader role, were followed by a computer algorithm with a high or low degree of synchrony. Participants (healthy controls) who were followed synchronously self-reported higher affective empathy (i.e., sharing emotions) relative to those who were followed asynchronously. Taken together, synchrony increases subjective understanding of the emotions of others (cognitive empathy) and possibly also self-reported sharing of the emotions of others (affective empathy). However, these studies relied on self-reported empathy measures. There are often considerable discrepancies between self-reported measures of empathy (e.g., using questionnaires) and objective measures of people' ability to read and share emotions. Several studies found little to no correlation between objective and self-reported empathy measures (Levenson and Ruef, 1992; Ickes, 1993; Realo et al., 2003; Jospe et al., 2020). Indeed, only a small portion of the variance in objective measures may be explained by self-reported questionnaires: around 1% according to some estimates (Murphy and Lilienfeld, 2019). This is not surprising if we consider that self-report questionnaires (but not objective measures) rely on metacognitive insight into one's capacities and are sensible to well-documented biases: social desirability (Sedikides et al., 2003) and the Dunning-Kruger effect (where poor performers overestimate their abilities and high performers often underestimate their abilities, Ames and Kammrath, 2004).

The effect of synchrony on objective measures of empathy remains less clear. The discrepancy between objective and self-reported empathy measures implies that we cannot simply extrapolate the findings from self-report measures to objective empathic performance. Studies that did use objective measures of empathy tended not to find effects of synchrony. For example, synchronous movements did not significantly affect participants' ability to attribute the correct emotions to a corresponding image of the eye region (Baimel et al., 2018). Using this same Reading the Mind in the Eyes task, Koehne et al. (2016) found no correlation with perceived synchrony (in a unilateral synchrony task). These findings are important but leave open one possibility.

The studies had participants rate emotions of unknown people in pictures, whereas the effects of synchrony may be specific to the synchronizing partners. Indeed, the issue of whether the effects of synchronous movements are specific to those we synchronize with is still open: some studies report that synchrony selectively boosts helping behaviors toward the people we synchronize with (Cirelli, 2018) while others show that moving in synchrony induces an effect that generalizes even to those who did not move in synchrony with us (Reddish et al., 2014, 2016). Thus, in the case of empathy, one would need to measure the accuracy or reading the emotions of the people that one synchronizes with. This is exactly what was done more recently, in a study using the Empathic Accuracy paradigm in which two partners first engage in a conversation and are then asked a series of questions on their own and their partner's feelings and thoughts. The study found that the degree of success in inferring others' emotions and thoughts (empathic accuracy) was not significantly associated with spontaneous behavioral synchrony during the conversation (Fujiwara and Daibo, 2021). Although highly relevant, this study relied on spontaneous behavioral synchrony which tends to be less stable than imposed synchrony (Richardson et al., 2005, 2007; Schmidt and Richardson, 2008). For this reason, it is possible that the resulting effects of synchrony on empathy were too small to detect. Imposing synchrony in a stable manner may affect empathic accuracy more robustly, as we will test here. Further, the Fujiwara and Daibo study measured accuracy for inferring both emotions and thoughts and so the absence of effect may be because synchrony has a different effect on awareness of thoughts (Theory of Mind) and awareness of emotions (empathy).

Studies on empathy have focused primarily on cognitive (emotion understanding) rather than affective (emotion sharing) empathy. Theoretical accounts predict that behavioral synchrony should lead to alignment of affective states (Shamay-Tsoory et al., 2019) but to our knowledge, this has been tested using subjective, not objective measures of emotion sharing. Using subjective measures, Koehne et al. (2016) found that participants self-reported more emotion sharing with synchronous vs. asynchronous partners. However, again this is a self-report measure, and it remains unclear whether when measured objectively, synchronous participants share more emotions.

In sum, synchrony affects subjective cognitive empathy, but no effects have been found using objective measures, possibly because they used spontaneous synchrony or stimuli other than the person we synchronize with. In the present study we asked dyads to synchronize with a metronome and then measured empathy toward the synchronization partner in order to investigate whether objective empathy (both cognitive and affective) is influenced by synchrony.

The present study also addresses the question of whether moving in synchrony affects tendency to attribute mental states to others, namely Theory of Mind (ToM) (Wimmer and Perner, 1983). In this study we explore this issue in adult participants whereas prior work on ToM, independent of synchrony, focused predominantly on children and atypical populations. Recent work shows that ToM continues to develop during adulthood (Apperly et al., 2010; Klindt et al., 2017) and new tasks have been developed to assess adults' actual and self-reported advanced ToM skills (Apperly, 2011; Devine and Lecce, 2021). Previous research offers some preliminary evidence that synchrony affects self-reported mentalizing. For example, participants who in small groups moved synchronously to a metronome increased the extent to which mental states are ascribed to the other members of the group (Baimel et al., 2018). Similarly, perceived synchrony, in a unilateral synchronization experimental task, correlated with the perceived ability to understand the thoughts and intentions of their partner (Koehne et al., 2016). Together, these studies suggest that moving in synchrony with a partner increases self-reported understanding of the partner's mental states. It remains unclear whether synchrony affects people's actual attribution of mental states using performance-based measures of ToM. Performance-based tasks differ from self-report questionnaires in that they do not assess people's beliefs about their own ToM but, rather, examine the extent to which people actually attribute mental states to selected stimuli such as characters in vignettes (e.g., Happé, 1994) or videos (e.g., Murray et al., 2017), or to abstract geometrical moving shapes (e.g., White et al., 2011). While emerging research has shown that self-reported questionnaires may correlate with performance-based measures (Bukowski and Samson, 2017; Clutterbuck et al., 2021), it is not clear whether the effects of synchrony found in self-reports extend to performance-based ToM measures. To date the only study conducted on this topic is that of Koehne et al. (2016). After having performed the unilateral synchrony task (see above), participants completed the Movie to Assess Social Cognition (MASC), a video-based task in which participants watch a short movie about four characters getting together for a dinner party and to answer to a series of questions concerning the characters' mental states (Dziobek et al., 2006). Authors found that individual performance in produced synchrony (follower's success in adjusting his or her movements to the leader to produce synchrony) were unrelated to performance in the MASC. Two features of this study should, however, be noted here. First, correlations are based on a restricted sample of 22 healthy controls; second, as the authors pointed out, there may have been too low variability in MASC scores to detect correlations with synchrony. In the present study we aimed to recruit a larger sample and employ a different performance-based ToM task to test whether synchrony affects ToM. The task chosen is the Triangle task (Castelli et al., 2000), that measures participants' attribution of intentionality as they describe a video of moving geometric shapes in absence of any contextual verbal or non-verbal cues other than movement.

In the present study we recruited participants who were divided into dyads that were unacquainted. These dyads met online through video conference and performed a series of periodic hands movement (clapping) paced by a metronome, either in synchrony or asynchrony with their partner. However, both these conditions involved rhythmic arm movements and fixed gaze position that may be perceived as unnatural. As a result, participants could experience these conditions as awkward on the one hand or as fun and engaging on the other hand. Such perceptions could affect the social affiliation measures that we collect here. Thus, to put the results from the synchrony and asynchrony conditions in perspective, we included a more conventional interaction: the small talk condition in which participants freely talked about a set of predefined questions. In this group, participants were not restricted in their arm, head and eye movements. Thus, this condition serves as a relatively ecological baseline to which any differences between synchrony and asynchrony can be interpreted. The aims of the study were to examine the effect of synchrony on (1) social affiliation (perceived similarity, closeness, likeability, and future friendship), (2) the tendency to attribute mental states and intentionality to others (ToM), and (3) on the accuracy of perceiving other's emotions and sharing them. Empathy was measured using the empathic accuracy paradigm, an ecological task that constitutes a relatively objectively measure of whether participants in dyads can accurately infer each other's emotions (cognitive empathy) and share those emotions (affective empathy). ToM was measured using two tasks: a self-report questionnaire (measuring the extent to which mental states were attributed to the dyadic partner) and a performance-based measure (measuring the degree of intentionality ascribed to abstract moving shapes in a video). The study was conducted entirely online during the COVID-19 pandemic in Italy (spring 2020) which was a period of a degree of imposed social isolation. To control for potential effects of this social isolation, we measured social contacts, wellbeing, and loneliness.

MATERIALS AND METHODS

Participants

One hundred twenty-six Young Adults Were Recruited Through Social Networks and the Newsletter of the Psychology Department. Participants Had a Mean age of 23.59 years (SD = 3.21, Range = 19–32 years) and Were Randomly Assigned to one of the three Experimental Conditions: Synchrony (*N* = 40; 30 Females), Asynchrony (*N* = 46; 35 Females) and Small Talk (*N* = 40; 30 Females). All Participants Were Fluent Italian Speakers. Criteria for Inclusion Were Written Consent and age Between 19 and 35 years. The Study Was Approved by the Ethics Committee of the Department of Brain and Behavioral Sciences of the University of Pavia (Approval # 048/20). Prior to Participation, all Participants Were Informed About the Aims of the Study and Signed the Informed Consent, According to the Declaration of Helsinki. The Dataset Is Available Online at osf.io/Jchzb/.

Procedure

Participants were contacted *via* mail and asked to complete a questionnaire assessing baseline variables: demographic information, quantity of social contacts, shyness, wellbeing, and loneliness. In the second phase, participants were paired in dyads according to the following rules: being unacquainted, close in age (maximum age difference was 3 years) and of the same gender. Dyads were randomly attributed to one of three experimental conditions: synchrony, asynchrony, and small talk. After the manipulation, all participants, first, took part in the empathic accuracy procedure, then completed the two ToM tasks (the Triangle task and the Mental State Attribution questionnaire) and, finally, filled out a series of questions evaluating social affiliation (closeness, similarity, degree of liking, and possibility of a future friendship; details below). The experimental procedure is represented in **Figure 1**.

The entire video call took ∼90 min.

Synchrony and Asynchrony Manipulation

In the synchrony condition participants were asked to make a cyclic movement with their hands (touching the palms of the hands and then putting them opened in front of the camera) in time with a metronome (periodic beep) sound that was presented through Zoom at the same tempo for both partners (65 beats per minute (bpm) for half the dyads and 55 bpm for the other half). These particular tempi were chosen for consistency with prior studies (Reddish et al., 2013, 2014). Participants were instructed to perform the movement continuously while looking at their partner. In the asynchrony condition participants received the same instructions and followed the same procedure as those belonging to the synchrony group. The only difference was that in the asynchrony condition, the two participants were received a different tempo (55 bpm and 65 bpm) (see **Figure 1**) and as a result their movements did not generally align in time. Participants in both these conditions were not allowed to talk to each other.

Immediately following the movements, participants were asked whether they had perceived Internet connection problems. Results showed that 13 participants in the synchrony group (32.5%) and 14 in asynchrony group (30.4%) reported that they perceived Internet connectivity issues. These numbers were not significantly different between groups ($X^2(2,85) = 0.08, p = 0.78$).

Small Talk Condition

In the small talk condition participants (instead of performing movements either in synchrony or asynchrony with their partner) took part in a semi-structured conversation based on 24 questions of the small talk task developed by Sedikides et al. (1999). The subjects were instructed to go through the 24 questions in order, taking turns answering one question. Participants were not restricted in their movements, and they could see each other during the conversation.

Empathic Accuracy

The empathic accuracy procedure (adapted from Blanke et al., 2016) consists of a semi-structured conversation in which participants are asked to talk, in turn, for 3 min about a positive and a negative event that happened in their life (**Figure 2**). The listener is allowed to interrupt the partner to ask questions. At the end of this 12-min conversation, the researcher showed participants the recorded video of their conversation twice, interrupting the video every 90 s ("tape stop"). At each tape stop, the researcher asked participants to report their own (in the first viewing) and estimate their partner's (in the second viewing) emotions answering the following questions: "How do you feel?" and "How does your partner feel?". Participants answered these questions for each of nine emotions (five positive: happy, excited, content, comfortable, balanced and four negatives: nervous, sad, uncomfortable, tense) using a 7-point scale ranging from 0 (not at all) to 6 (very much) (see Measures). The answers given by the subjects were confidential (invisible to their dyadic partner) (see

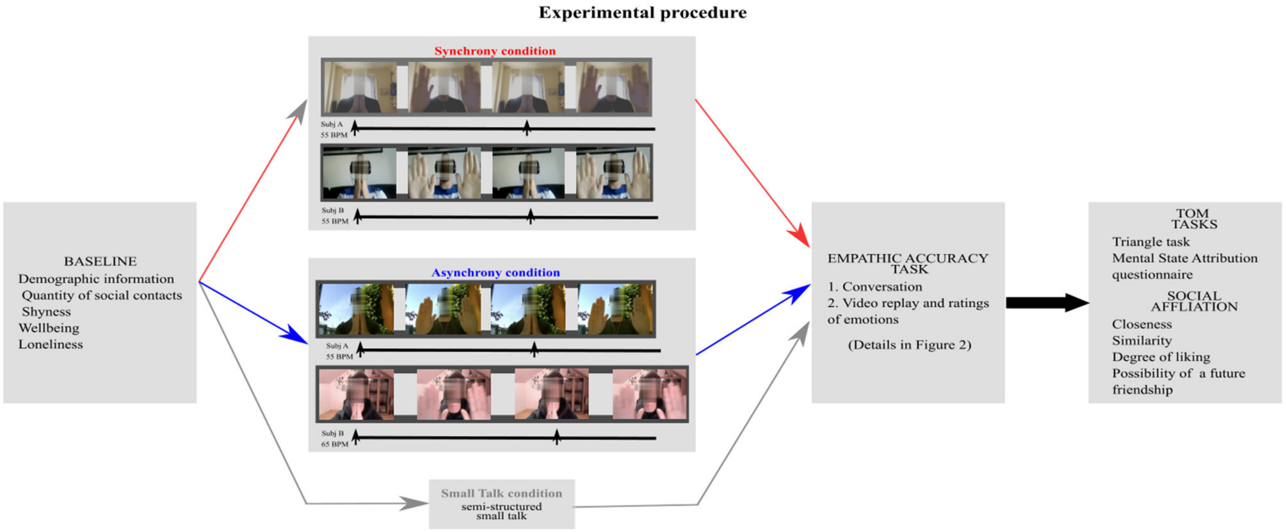


FIGURE 1 | Experimental procedure. Participants first completed a questionnaire assessing baseline variables, second, engaged in synchronous/asynchronous movement or small talk, third, completed the Empathic accuracy procedure and finally, completed the ToM tasks and a series of questions evaluating social affiliation. In the synchrony and asynchrony conditions subjects clapped their hands in time with a metronome sound presented *via* headphones while looking at their partner. In the synchrony condition the metronome had the same BPM (beats per minutes) for both partners. In the asynchrony condition the metronome had a different BPM for the partners. Movements were therefore aligned in time in the synchrony but not in the asynchrony condition. In the figure the lines represent the time and the arrows represent when the metronome sound occurred, in time with which participants clapped their hands. In the small talk condition, participants took part in a semi-structured conversation.

Figure 2). After completing the empathic accuracy procedure, participants were administered the two ToM tasks, the Triangle task and the Mental State Attribution questionnaire, and the social affiliation questionnaires.

Measures

Baseline Variables

General Information Questionnaire

We asked participants to report on their age, gender, and general information about the social situation that they were experiencing (i.e., days of isolation, number of times they went out during the last week).

Social Contacts

We administered an in-house questionnaire to assess the frequency of social contacts (e.g., phone call, texting, and videocalls) during the last week. Possible answers range from 0 (never) to 4 (more than once a day) and were summed into a total score ranging from 0 to 70 ($\alpha = 0.64$).

Wellbeing

We used the Italian version of the Warnick-Edinburgh Mental Well-Being Scale (WEMWBS; Gremigni and Stewart-Brown, 2011). WEMWBS is a 14-item scale covering both hedonic and eudaimonic aspects of mental health including positive affect (feelings of optimism, cheerfulness, and relaxation), satisfying interpersonal relationships and positive functioning (energy, clear thinking, self-acceptance, personal development, competence, and autonomy). Participants were required to tick the box which best described their own experience over the past 2 weeks using a 5-point Likert scale (1 = none of the time; 5 = all of the time). Item scores were summed into a single total score of wellbeing ranging from a minimum of 14 to a maximum of 70, with higher scores representing higher levels of mental wellbeing ($\alpha = 0.85$).

Loneliness

Participants filled out the Revised UCLA Loneliness Scale (R-UCLA; Russell et al., 1980). This scale consisted of 20 items, 10 positively (e.g., "There are people I can turn to") and 10 negatively worded (e.g., "I feel isolated from others"). Answers were based on a 4-points Likert scale ranging from 1 (never) to 4 (often). Once items were reverse scored, all of them were summed to create an overall index of loneliness, ranging from a minimum of 20 to a maximum of 80 with higher scores indicating greater loneliness ($\alpha = 0.79$).

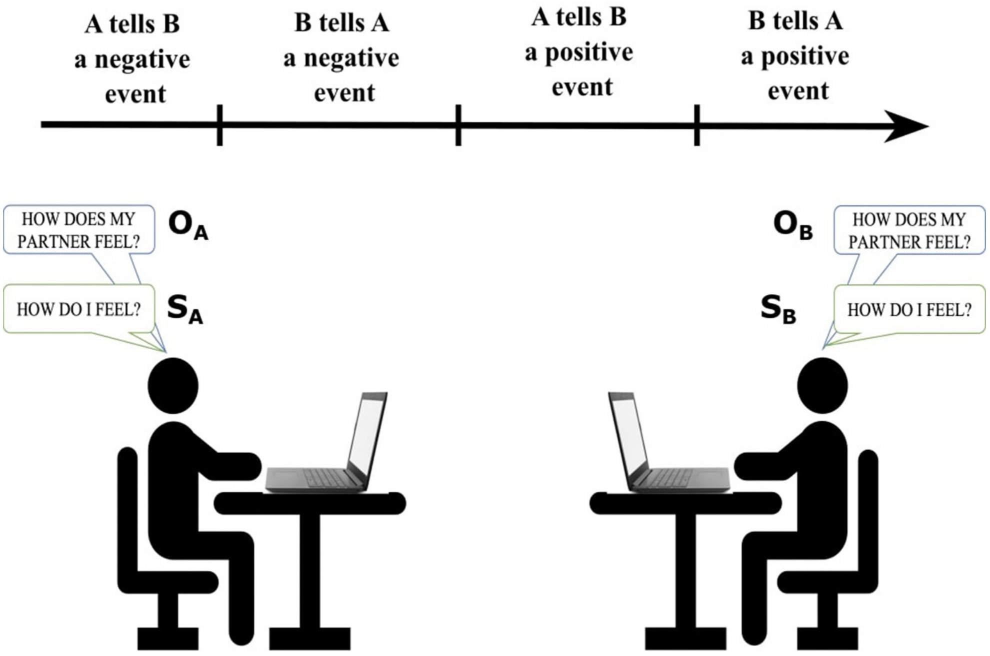
Shyness

Participants responded to the Italian version of the Revised Cheek and Buss Shyness Scale (RCBS-14; Marcone and Nigro, 2001). The scale consists of 14 items to which subjects responded on a 5-point Likert scale from 0 (completely disagree) to 4 (completely agree). Responses were summed into a single shyness score (range 0–56) ($\alpha = 0.89$).

Variables of Interest (Post-manipulation)

Empathy

This was measured using the empathic accuracy task (adapted from Blanke et al., 2016) which consists of a semi-structured conversation between two participants (see procedure 2.2.1). On



Tape stop	Emotion	S_A	O_A	S_B	O_B	EA_A	EA_B	EC
1	Happy	0	2	0	1	2	0.5	0
1	Comfortable	3	5	6	4	0.5	0.5	4.5
1	Nervous	3	3	2	5	0.5	2	0.5

FIGURE 2 | Empathic accuracy procedure and an example of empathic scores computation. Two participants (A, B) took part in a semi-structured conversation in which both participants talk about positive and negative events in their life. At the end of talk, the researcher showed participants the recorded video of their conversation twice, interrupting the video at eight time points (tape stops). At each tape stop, the researcher asked participants to rate their own (in the first viewing) and their partner's (in the second viewing) emotions. Based on these answers, we computed empathic accuracy (EA) and emotional congruence (EC) as shown, for an example portion of the data in the table. S_A, self-reported feelings of participant A; S_B, self-reported feelings of participant B; O_A, other-rating of A: estimation by A of B's feelings; O_B, other-rating of B: estimation by B of A's feelings; EA_A, empathic accuracy of participant A; EA_B, empathic accuracy of participant B; EC, emotional congruence of the dyad.

the basis of participants' answers to the questions of "How do you feel?" and "How does your partner feel?," we computed a score of *empathic accuracy* as the similarity between the participant's self-reported feelings and the empathizer's judgment of the experimental partner's feelings (cognitive empathy) and *emotional congruence* as the similarity between the two participants' self-reported feelings (affective empathy) (**Figure 2**). Specifically, for empathic accuracy, we calculated the sum of squared differences of the judgment of the empathizer and the self-report of the partner across the eight tape stops for each emotion, which were then averaged to yield one empathic accuracy score for positive and one for negative emotions in each participant. The reason positive and negative emotions were kept separate is because empathy for positive and negative emotions are considered as two distinct but related constructs with different properties and correlates (Rothbart et al., 2000; Sallquist et al., 2009). Analogously, emotional congruence was calculated *via* the sum of squared differences between both partners' emotion ratings across the tape stops (see **Figure 2**). Note that while empathic accuracy yielded an individual score for each participant, emotional congruence yielded a single score per dyad.

Theory of Mind (ToM)

ToM was measured using a self-report questionnaire, the Mental State Attribution questionnaire (Baimel et al., 2018), and a performance-based task, the Triangle task (Castelli et al., 2000).

The Mental State Attribution questionnaire consists of 15 items evaluating participants' tendency to view the experimental partner as someone who owns mental states (emotions, thoughts, desires) (Baimel et al., 2018). Responses were on a 7-points scale (1 = completely disagree; 7 = completely agree; summed score range: 15–105; $\alpha = 0.87$).

The Triangle task (Castelli et al., 2000) evaluates the extent to which people attribute intentionality to geometric shapes on the basis of their movements. It has been shown to reliably differentiate between high-functioning ASD groups and verbal ability matched control groups (Abell et al., 2000; Murray et al., 2017) and has been used in studies with neurotypical adults (for example Devine and Hughes, 2019). From the three categories of videos (random, goal-directed and ToM) in the original study, the present study selected two ToM videos of moving geometric shapes (triangles) that behaved in such a way as to imply teasing and joking. Each animation lasted ∼40 s. After watching each video clip, participants were asked to write down what happened in each clip. The score for each clip reflected the degree to which participants described the video in terms of complex intentional mental states, according to the original guidelines (Castelli et al., 2000, **Appendix II**, Intentionality score). The intentionality score for each description ranged from 0 (no deliberate action, e.g., "bouncing", "rotating") to 5 (deliberate action aimed at affecting another's mental state, e.g., "persuading", "pretending", and "deceiving"). Two raters independently coded 25% of the responses and interrater agreement was established using Cohen's kappa ($\kappa = 0.77$). All remaining responses were coded jointly by the raters. Disagreements were resolved through discussion between the raters. During this entire procedure the coders were blinded to the experimental condition. The summed score for the two videos could range from 0 to 10 points.

Closeness

We assessed how close each participant felt to their experimental partner using the Inclusion of Other in the Self Scale (IOS) (Aron et al., 1992). Participants were asked to report how close they felt to the partner by picking one out of seven "Venn diagrams": each was a pair of more or less overlapping circles (**Figure 4D**). On one end of the continuum, the circles are completely separate, and, on the other end, the circles are virtually entirely overlapping (Range: 1–7 with higher values meaning greater closeness).

Perceived Similarity, Liking and Future Friendship

Participants rated on a 9-point scale from 1 (not at all similar) to 9 (very similar) (Range: 1–9) the following statement: "How similar do you feel to the participant with whom you take part in this study?" (*perceived similarity*). Participants responded on a 9-point scale from 1 (not at all) to 9 (very much) the following two statements: "How much do you like the participant with whom you take part in this study?" (*likeability*) and "In the future, to what extent do you feel that you could be friends with the participant with whom you take part in this study?" (*future friendship*) (Sedikides et al., 1999).

Data Analysis

We first removed outliers in each dependent variable using the boxplot rule (Tukey, 1977): a data point is considered an outlier if it is more than 1.5 times the interquartile range above the upper quartile or below the lower quartile.

We performed a randomization check by running a series of ANOVAs with experimental group (synchrony, asynchrony, and small talk) as the independent variable and each baseline variable in turn as dependent variable in order to investigate whether there were differences between experimental groups at the outset (see **Table 1**).

To test our main hypotheses, we performed a series of ANCOVAs with experimental condition (synchrony, asynchrony, and small talk) as the between-participants factor, variables of interest (see details below) as dependent variables and gender as covariate (to control for gender differences). For each variable of interest, we further checked whether there was a significant correlation with any of the baseline variables (general information, social contacts, shyness, loneliness, and wellbeing) and, if so, these were included as covariates. Follow-up tests were performed using planned orthogonal contrasts: first, we investigated the effect of synchrony using a synchrony vs. asynchrony contrast and, second, we contrasted synchrony and asynchrony together vs. small talk. The rationale for the planned latter contrast is that synchrony and asynchrony conditions involve precisely prescribed rhythmic movements that are potentially experienced as unnatural and rigid, in similar ways, whereas the small talk condition is a more common, ecological interaction. For reference, separate contrasts (synchrony vs. small talk and asynchrony vs. small talk) are reported in the **Supplementary Materials** section. Empathic accuracy and emotional congruence were analyzed using a series of ANCOVAs controlling for gender with experimental condition (synchrony, asynchrony, and small talk) as between-participants factor and the valence of emotion (positive and negative) as within-subject factor. Where significant, we then examined the effect of experimental condition on positive and negative empathic indexes separately using ANOVAs. Finally, when the ANOVA follow-up contrasts were not significant for contrasts of interest (synchrony vs. asynchrony) in the empathic measures (empathic accuracy and emotional congruence), we calculated the Bayes Factor BF_{10} (i.e., evidence for alternative vs. null hypothesis). The Bayes Factor, when smaller than 1, quantifies the amount of evidence in favor of the null hypothesis, that there is no difference between groups. Benchmark scores: BF_{10} between 1 and 1/3 are considered to be weak, between 1/3 and 1/10 are considered moderate, and >1/10 are considered strong evidence in favor of the null hypothesis (Jeffreys, 1961).

We report η_p^2 partial effect sizes (Keppel, 1991).

RESULTS

Preliminary Analyses and Descriptive Statistics

Randomization check: ANOVAs showed no significant differences between the three groups on any of the baseline variables (all $ps > 0.07$, **Table 1**), indicating that there was no evidence for group differences at the outset.

Comparing values on the wellbeing scale with normative scores, we found that for the majority of our sample, wellbeing was above clinical levels (70.6%). Of the remaining 29.3%, 12.6% of participants reported a level of wellbeing indicating a probable depression and 16.7% a possible depression.

Descriptive statistics of the post-manipulation focus variables are reported in **Table 2**.

TABLE 1 | Descriptive statistics and group comparisons (ANOVA) on baseline variables.

Measure	Synchrony (n = 40)			Asynchrony (n = 46)			Small talk (n = 40)			ANOVA	
	M	SD	Range	*M*	SD	Range	*M*	SD	Range	F (df$_{\text{num}}$, df$_{\text{den}}$)	*p*
Age	23.90	2.57	19–30	23.74	3.49	19–32	23.10	3.47	19–31	0.69 (2, 123)	0.499
Education	2.60	0.78	1–4	2.50	0.59	2–4	2.58	0.84	2–5	0.22 (2, 123)	0.805
Isolation	43.37	10.27	30–68	48.50	9.28	36–85	43.69	10.04	25–65	2.72 (2, 94)	0.071
Going out	1	1.28	0–4	1.39	1.20	0–4	1.30	1.22	0–4	1.15 (2, 123)	0.320
Social	15.48	4.50	4–27	14.94	4.11	5–24	15.2	4.12	3–22	0.17 (2, 123)	0.841
Shyness	38.33	4.65	30–50	39.87	4.97	31–56	38.90	6.32	19–49	0.40 (2, 123)	0.399
Wellbeing	47.98	7.51	32–62	48.28	8.51	27–69	48.68	5.99	35–62	0.09 (2, 123)	0.500
Loneliness	51.95	4.81	40–60	52.98	3.73	46–61	52.68	3.72	43–60	0.70 (2, 123)	0.915

ANOVA, analysis of variance; Isolation, Days of isolation; Going out, number of times they went out during the last week; Social, social contacts.

TABLE 2 | Descriptive statistics on post-manipulation variables.

Measure	Synchrony (n = 40)			Asynchrony (n = 46)			Small talk (n = 40)		
	M	SD	Range	*M*	SD	Range	*M*	SD	Range
MSA	5.90	0.60	4.53–7	5.70	0.54	4.27–6.93	5.86	0.62	4.40–7
Intentionality	7.38	1.88	2–10	6.17	2.24	1–10	6.5	2.21	2–10
IOS	3.58	1.24	1–6	2.26	1.07	1–5	3.23	1.25	1–6
Similarity	6.13	1.83	1–9	5.30	1.62	2–8	5	1.81	0–8
Likeability	8.08	0.81	7–9	7.76	1.01	5–9	7.61	0.90	6–9
Future Friendship	6.91	1.40	2–9	6.85	1.15	4–9	6.13	1.77	2–9
EA	0.87	0.35	0.31–1.80	0.87	0.32	0.24–1.46	0.72	0.40	−0.04 to 1.87
EC	0.59	0.32	0.06–1.32	0.71	0.49	−0.13 to 1.55	0.55	0.40	−0.39 to 1.25

MSA, mental state attribution; Intentionality, theory of mind score in the triangle task; IOS, inclusion of other in self; EA, empathic accuracy; EC, emotional congruence.

Manipulation Check

In order to assess the amount of synchrony in the experimental groups (nominal synchrony and asynchrony conditions) we performed an analysis that was inspired by Motion Energy Analysis (Ramseyer, 2020). For each dyad, we extracted the part of the video recording where participants made movements paced by the metronome. We analyzed each of the two persons' video separately, converted into grayscale (**Figure 3A**). For each consecutive two frames, we calculated the pixel-by-pixel intensity difference. Taking the mean absolute value of these differences across the frame, this yielded a single value estimating the overall amount of change in the frame relative to the next. The corresponding time course was filtered (5th order Butterworth bandpass filter 0.75–1.25 Hz) to extract the periodicity in the vicinity of the pacing frequency (**Figure 3B**). In order to account for possible small delays in the signal, we calculated the maximum Pearson cross-correlation between the signals with a maximum shift of 25 frames (1 s). This yielded a single Pearson correlation value per dyad which was Fisher r-to-z transformed and compared between synchrony and asynchrony conditions (**Figure 3C**). The image change time courses showed greater correlation in the synchrony condition (Pearson z mean = 0.59, SD = 0.28) than in the asynchrony condition (Pearson z mean = 0.32, SD = 0.20) [t (41.50) = 3.81, $p < 0.001$, Cohen d = 1.11, 95% CI (0.47, 1.76)]. This suggests that the nominal synchrony dyads indeed moved more synchronously than dyads in the nominal asynchrony condition.

Synchrony and Social Affiliation

We found a significant effect of the experimental group on perceived similarity, F (2, 122) = 4.14, p = 0.014, η_p^2 = 0.68 (**Figure 4A**). Planned contrasts revealed statistical trends toward significance with participants in the synchrony condition rating their partners as more similar to themselves than participants in the asynchrony condition, t (122) = 2.17, p = 0.063, and participants taking part in the synchrony and asynchrony groups with respect to those belonging to the small talk one, t (122) = 2.13, p = 0.067. The ANOVA on likeability scores showed a statistical trend toward significance for the effect of the experimental group, F (2,110) = 2.82, p = 0.063, η_p^2 = 0.45 (**Figure 4B**). Planned contrasts showed no significant difference between synchrony and asynchrony groups t (110) = 1.18, p = 0.42. The synchrony and asynchrony vs. small talk contrast was marginally significant, with synchrony/asynchrony participants condition showing higher scores than those in the small talk condition, t (110) = 2.16, p = 0.64. For perceived closeness, results revealed a significant main effect of experimental group F (2, 122) = 3.07, p = 0.050, η_p^2 = 0.05 (**Figure 4C**). Planned contrasts showed that the synchrony group reported more closeness than the asynchrony group, t (122) = 2.48, p =

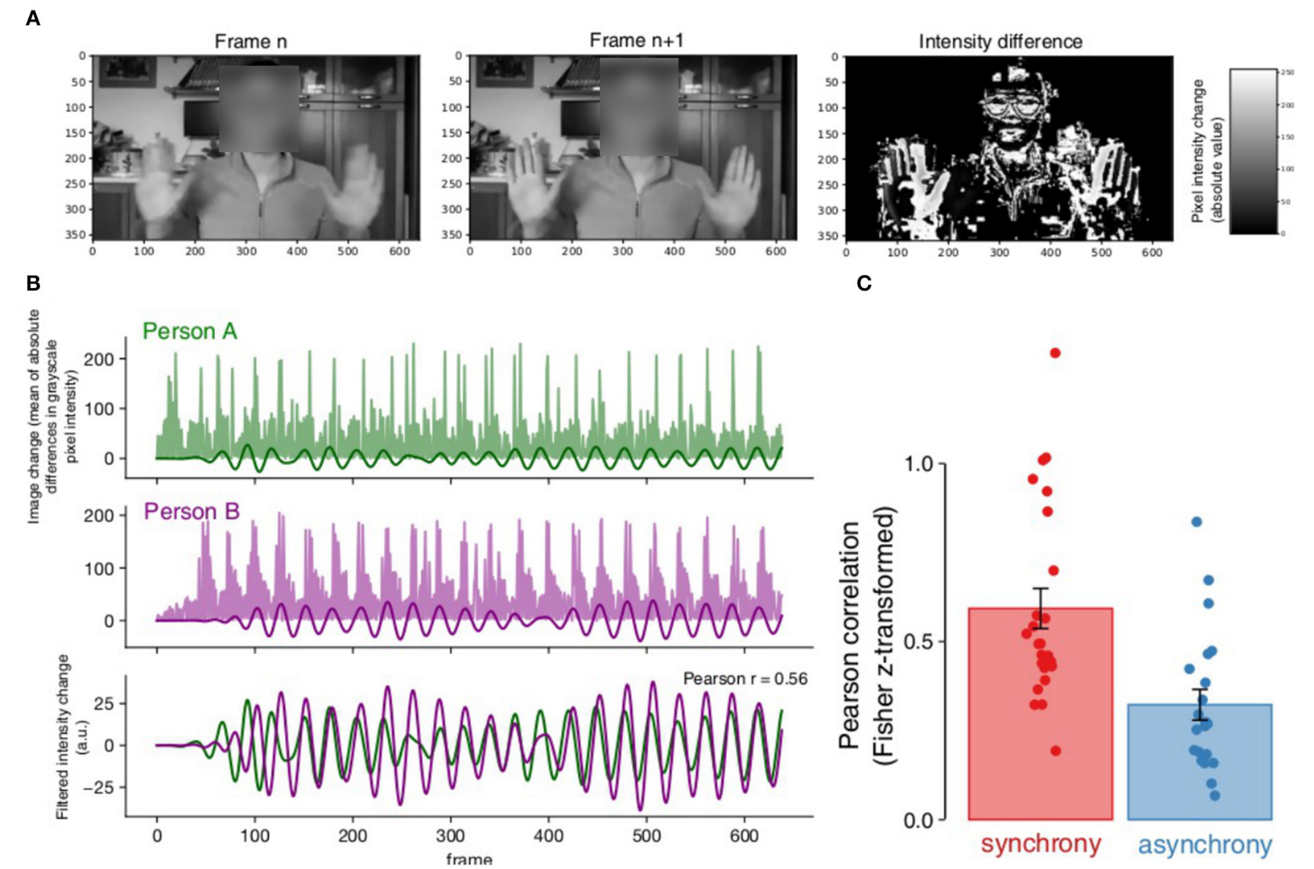


FIGURE 3 | Manipulation check. Manipulation check indicating that the nominal synchrony dyads moved more in synchrony than the asynchrony condition. See text for detail. **(A)** Differences in pixel intensity were calculated across the image and averaged. **(B)** Raw mean absolute image change showed periodic patterns in both participants (bar graph in the background) that were extracted using bandpass filtering (line in the foreground). Pearson correlation was calculated between these traces (bottom panel). **(C)** The dyads in the nominal synchrony condition showed greater correlation among their movement traces than participants in the asynchrony condition. Bars represent average, error bars indicate standard error of the mean and dots indicate individual dyads.

0.029. The contrast between synchrony/asynchrony and small talk groups was not significant, t (117) = 0.80, $p = 0.67$. No significant difference between groups was found on the future friendship question, F (2, 121) = 1.66, $p = 0.20$, $\eta_p^2 = 0.03$.

Overall, these data showed that participants in the synchrony condition were more likely to perceive their experimental partner as close and, marginally, as more similar than in the asynchrony group but did not rate more liking or future friendship possibility.

Synchrony and Empathic Accuracy, Emotional Congruence

For empathic accuracy, we first conducted a 3 x 2 mixed ANCOVA with group as between-subject variable, valence of the emotions (positive and negative) as within-subjects factor and empathic accuracy as dependent variable (controlling for gender). Results showed no significant effect of the experimental group, F (2, 120) = 1.30, $p = 0.275$, $\eta_p^2 = 0.02$, and no significant interaction, F (2, 120) = 1.75, $p = 0.178$, $\eta_p^2 = 0.03$ (**Figure 4E**). A significant effect was found for the valence of the emotions, F (1, 120) = 19.75, $p < 0.001$, $\eta_p^2 = 0.14$, indicating that empathic accuracy was greater for negative than for positive emotions. Since the main effect of group was not significant, we proceeded to calculate the Bayes Factor of the principal contrast of interest between synchrony and asynchrony and found $BF_{10} = 0.23$ for positive and $BF_{10} = 0.29$ for negative emotions. This indicates moderate evidence in favor of the null hypothesis that there is no difference between synchrony and asynchrony groups in empathic accuracy for both positive and negative emotions.

For emotional congruence there was no significant effect of group, F (2, 118) = 1.76, $p = 0.176$, $\eta_p^2 = 0.03$, but a significant main effect of the valence of the emotions, F (1, 118) = 27.68, $p < 0.001$, $\eta_p^2 = 0.19$, with emotional congruence being greater for negative emotions than for positive emotions (**Figure 4F**). The interaction between experimental group and valence of emotions was significant, F (2, 118) = 3.71, $p = 0.027$, $\eta_p^2 = 0.06$. We then followed up with two separate ANCOVAs on positive and negative emotional congruence, respectively. For positive emotional congruence, the effect of group was not significant, F (2, 118) = 0.23, $p = 0.79$, $\eta_p^2 = 3.92$, but for negative

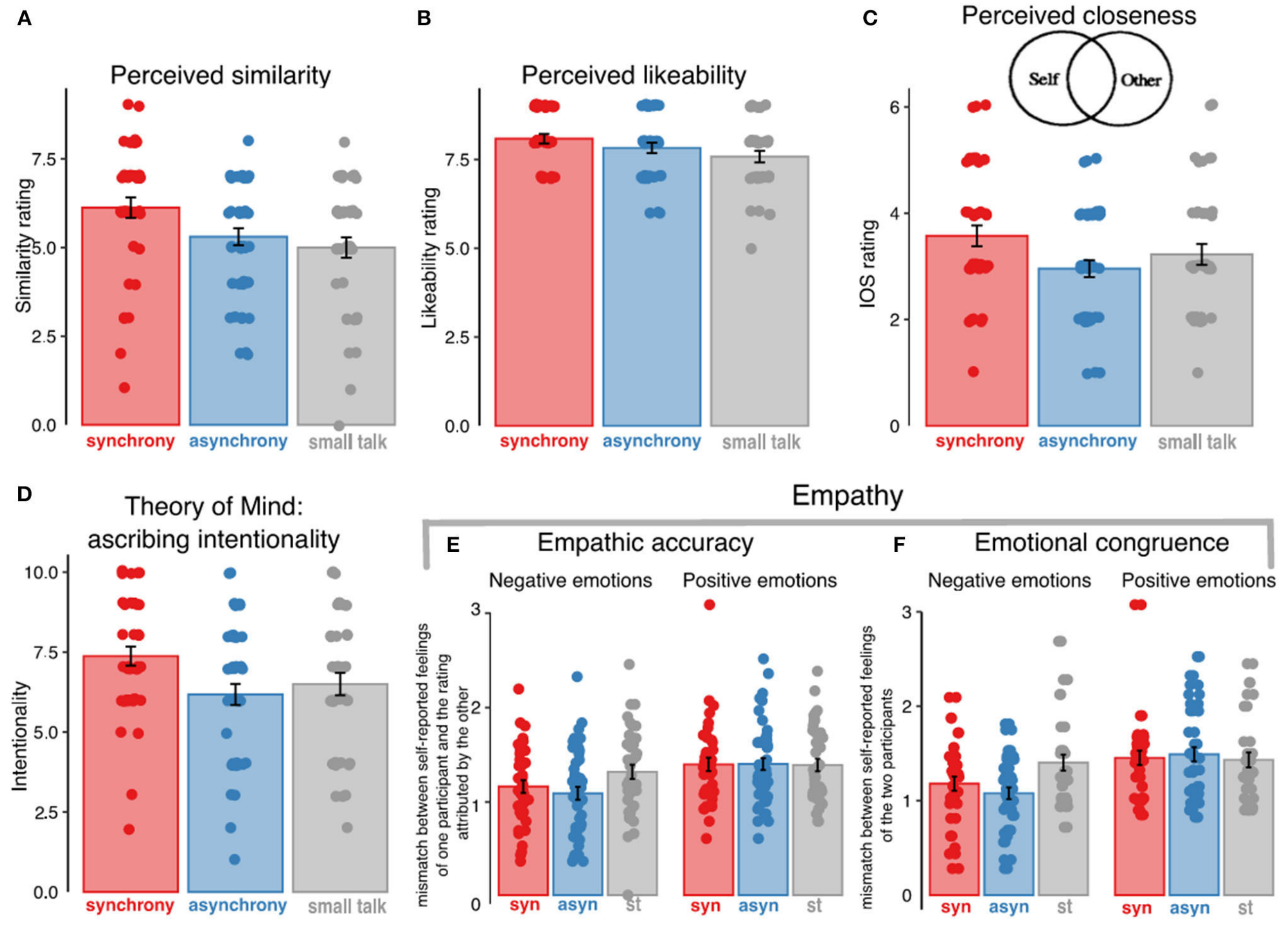


FIGURE 4 | Effects of synchrony on social affiliation, empathy and theory of mind. Participants in the synchrony group reported greater similarity **(A)**, likeability **(B)**, and closeness **(C)** to their partners than participants in asynchrony and small talk groups. Closeness was measured using the Inclusion of Other in the Self (IOS) scale of which a sample item is shown in the inlay. Participants in the synchrony group attributed greater intentionality to triangles in a video **(D)**. For the empathic measures, empathic accuracy **(E)** and emotional congruence **(F)** results are shown separately for negative and positive emotions, and no group differences were found. In all panels dots represent participants' single scores; bars represent group averages and error bars the standard error of the mean. syn, synchrony; asyn, asynchrony; st, small talk.

emotional congruence it was, F (2, 118) = 5.53, $p = 0.005$, $\eta_p^2 = 0.09$. Planned group contrasts for negative emotional congruence revealed no significant difference between synchrony vs. asynchrony group, t (118) = 1.05, $p = 0.50$, but a significantly greater emotional congruence in the synchrony and asynchrony vs. the small talk group, t (118) = −3.11, $p = 0.005$. In sum, we did not find differences in emotional congruence between synchrony and asynchrony groups, whereas negative emotional congruence was greater in synchrony/asynchrony groups relative to the small talk. To assess the evidence for the finding that emotional congruence does not differ between groups, we calculated the Bayes Factor of the difference between synchrony and asynchrony groups and found $BF_{10} = 0.24$ for positive (moderate evidence) and $BF_{10} = 0.37$ (some evidence) for negative emotions. Overall, synchrony and asynchrony groups did not differ in assessing or sharing others' emotions.

Synchrony and Theory of Mind

The ANCOVA (controlling for gender) on the Triangle intentionality attribution scores showed a significant main effect of experimental group, F (2, 122) = 3.39, $p = 0.028$, $\eta_p^2 = 0.06$ (**Figure 4D**). Planned contrasts revealed that participants in the synchrony condition were more likely to attribute intentions to the triangles than participants in the asynchrony condition, t (122) = 2.65, $p = 0.009$. No significant difference was found between the synchrony and asynchrony vs. the small talk group, t (122) = 0.71, $p = 0.73$. For the Mental State Attribution questionnaire, no significant differences between groups were found, F (2, 120) = 1.49, $p = 0.23$, $\eta_p^2 = 0.02$. Overall, these results showed that participants in the synchrony group showed greater tendency to describe the video of the triangles in mental state terms than in the asynchrony group, but we did not find evidence that they were more likely to see other people as carrying mental states.

DISCUSSION

The present study investigated the effect of synchronous movement on social affiliation, empathy and ToM. We tested unacquainted participants who met on-line in dyads and performed 3 min of synchronous or asynchronous movements, or a semi-structured small talk conversation. We examined self-reported social affiliation with the dyadic partner (similarity, closeness, likeability, possibility of a future friendship), ToM (attribution of intentionality and mental states, using an objective and a subjective measure) and objective measures of empathy (empathic accuracy and emotional congruence). First, we found that participants in the synchrony group reported greater closeness to their partner relative to participants in the asynchrony and small talk groups, and a statistical trend toward greater similarity. Second, participants in the synchrony group were more likely to attribute intentions to abstract moving shapes than participants in the asynchrony and small talk groups. No differences were found between groups in attributing mental states to their partners. Finally, participants in the synchrony and asynchrony groups showed similar levels of accuracy in estimating (empathic accuracy) and sharing (emotional congruence) of their partner's emotions.

Synchrony and Social Affiliation

The present study found that the synchrony group reported greater closeness toward their partner relative to the asynchrony group, in line with prior in-person studies, whereas for a number of other social affiliation measures (similarity, likeability and future friendship) results were only marginal or absent. This suggests that in online encounters at least a subset of in-person effects of synchrony on social affiliation can be replicated.

Our finding that synchrony increases perceived closeness fits with existing studies that have typically been conducted in person (Paladino et al., 2010; Vacharkulksemsuk and Fredrickson, 2012; Reddish et al., 2013; Fessler and Holbrook, 2014; Lumsden et al., 2014; Dong et al., 2015; Tarr et al., 2016). Taken together these results show that moving in synchrony makes people feel closer to each other and this is true both when participants met online and offline. The effect of synchrony on closeness is in accordance with the self-other blurring hypothesis. According with this view, synchronizing with someone, compared to other coordinated behavior such as asynchronous or sequential action, blurs the boundaries between the self and other (Hove, 2008). This is thought to be because typically during synchronous movement, two people perform the same movement at the same time. This match between one's own action and the observation of another performing the same action makes it more difficult for the brain to distinguish between self and other (Paladino et al., 2010; Mazzurega et al., 2011; Tarr et al., 2014; Rennung and Göritz, 2016). This blurring of the self-other boundary would lead to greater perceived closeness or even a sense of oneness with a group (Swann et al., 2012). As for similarity, our results are partially in line with previous literature which reported an increase of the sense of similarity after synchronizing with someone compared to asynchronous or control conditions (Wiltermuth and Heath, 2009; Schachner and Garvin, 2010; Valdesolo et al., 2010; Valdesolo and DeSteno, 2011; Dong et al., 2015). The present study also indicated a trend for greater similarity in the synchrony group (relative to the asynchrony group) although this did not reach statistical significance. With regard to likeability, our data did not replicate a prior finding of an increase in liking after synchronous movement (Valdesolo and DeSteno, 2011).

We did not find an effect of synchrony on the perceived possibility to develop a future friendship with the experimental partner. As far as we know, our study is the first one testing whether this indicator of social affiliation is affected by synchrony. We expected participants in the synchrony group to be more willing to become friends than participants in the asynchrony group. This is because synchrony typically increases a range of social affiliation dimensions (Hove and Risen, 2009; Paladino et al., 2010; Valdesolo et al., 2010; Vacharkulksemsuk and Fredrickson, 2012; Reddish et al., 2013; Tarr et al., 2015, 2016) that presumably make one more likely to want to form a future friendship (Sedikides et al., 1999). However, we were not able to find support for this hypothesis.

This pattern of findings may reflect one of two hypothetical scenarios. A first possibility is that in-person, synchrony can affect a range of social affiliation measures, whereas online it affects only closeness. We speculate that the reason other affiliation measures (similarity, likeability) may not be affected by online synchrony in the same way as in-person synchrony is because of a lack of relevant visual cues, such as eye contact and physical proximity. Indeed, previous literature suggested that during in-person interactions, similarity and likeability are sensitive to such information (Peters, 2007). However, it remains challenging for this account to explain why the effect of online synchrony would be specific to closeness and not hold for related measures such as similarity and likeability. A second hypothetical scenario is that online synchrony actuality affects all measures of social affiliation, but the effects on likeability and the possibility of a future friendship were smaller and, therefore, did not reach significance here. This account is in line with theories of synchrony's social effects in which synchrony should affects multiple measures of social affiliation across the board (Hu et al., 2022). It remains unclear whether the effect on likeability and the possibility of a future friendship would be smaller. Since prior literature has typically merged all these variables (similarity, closeness, etc.) into a single, aggregate social affiliation measure, we do not have prior estimates for the effect sizes on the individual variables.

Our study is the first, to our knowledge, to document the social effects of synchrony in people meeting through video conferencing. There are some distantly related studies that found that synchronous movements between avatars (stick figures) can lead to greater perceived closeness and sympathy ratings (Stupacher et al., 2017a,b, 2020, 2021). If indeed such results rely on similar synchrony-to-social processes as operating between humans, as is sometimes tacitly assumed, then this lends credence to the idea that social effects of synchrony are not restricted to humans meeting in person. However, these studies differ in important ways from the present work, that makes such extrapolations tentative.

To summarize, our findings suggest that synchrony increases closeness in online environments. On the contrary, findings of other social affiliation measures were less clear: no detected difference in likeability and future friendship and only a statistical trend on similarity.

Synchrony and Empathy

Our data showed no difference between synchrony and asynchrony conditions for both empathic accuracy - the accuracy in understanding other's emotions - and emotional congruence - sharing emotions with another person.

It has been proposed that moving in synchrony would be associated with greater emotion sharing (Shamay-Tsoory et al., 2019). Indeed, on a subjective level this has been confirmed by a study in which participants taking part in a unilateral synchronization estimated that they shared emotions with their partners more than participants in an asynchrony condition (Koehne et al., 2016), although (Baimel et al., 2018), asking a similar question, did not find this effect. Here we tested whether this effect may hold on an objective level as well, by directly comparing the ratings of felt emotions by the two partners (emotional congruence). We found no difference between the synchrony and asynchrony conditions. Taken together, this suggests that although participants may have thought they shared the emotions of their partner (based on prior work), they did not actually do so (based on the present study). Synchrony may, thus, introduce a positive subjective bias in emotional congruence, making us believe we share more emotions with others than we really do. We speculate that this positive subjective bias may help us feel closer to the people we synchronize with, and that it can perform this function without requiring that we actually feel the same. Since in this study we did not collect subjective measures of emotion sharing we cannot test this association between closeness and subjective emotion sharing directly. The mismatch between subjective and objective measures of emotion sharing is reminiscent of similar mismatches that have been documented in the empathic accuracy literature. Indeed, subjective measures of empathic accuracy (thinking we know what the other feels) often differ from objective measures of empathy (actually knowing what the other feels) (Zaki et al., 2008; Murphy and Lilienfeld, 2019). If indeed synchrony affects subjective but not objective emotion sharing, future theoretical accounts of synchrony may need to draw this distinction and explain why that is the case.

In terms of accuracy of understanding others' emotions (empathic accuracy), prior studies like us did not find an effect of synchrony. However, empathic accuracy was typically measured using tasks that evaluate the extent to which participants correctly identified the emotions of people other than the synchronizing partners, such as for example when inferring emotions from a picture of somebody's eyes (Baimel et al., 2018). This left open the possibility that synchrony selectively boosts empathy toward the people we synchronize with (as has similarly been demonstrated in the case of helping behaviors, Cirelli et al., 2014; Cirelli, 2018), which is what we tested here. However, empathic accuracy toward the synchronization partner was not significantly different between the synchrony and asynchrony conditions. One other study focusing on spontaneous not imposed synchronization, investigated empathic accuracy toward the synchronization partner (Fujiwara and Daibo, 2021) and similarly found no relation to spontaneous synchronization. This study used a composite measure of empathic accuracy that included awareness of both thoughts and emotions. As a result, it was not clear whether synchrony might have specifically affected empathy for emotions. Our result provides evidence that this is not the case. Taken together, converging lines of evidence including our study reveal that synchrony has little if any effect on empathy, regardless of how synchrony was achieved (spontaneous vs. imposed) or toward whom empathy was directed (synchrony partner or others).

The lack of effect of synchrony on empathic accuracy in our study may help nuance more broad-stroke claims that effects of prolonged music training on objective measures of empathy are mediated by synchrony. Long-term music training has been associated with some effects on empathic functioning (Thompson et al., 2003; Rabinowitch et al., 2013) and some works have speculated this is driven by synchrony inherent in the musical training (Rabinowitch, 2017). However, other components of long-term music training are likely to be responsible for these boosts in empathy. One component may be musical material itself. Indeed, studies on social affiliation show that presenting music, as opposed to a simple metronome or silence, leads to greater closeness and likeability, and that this is true regardless of synchrony (Stupacher et al., 2017a). Perhaps a similar knock-on effect would hold for empathy, namely that regardless of synchrony, music would boost empathic accuracy. This could explain why music training could promote empathic accuracy when synchrony alone does not. Another component is the long-term nature of the music training tested in the aforementioned studies. Indeed, improving empathic accuracy by means other than synchrony or music, usually takes extended periods of time (Mascaro et al., 2013; Lobchuk et al., 2016; Kraus, 2017; Haut et al., 2019) except for very short pharmacological interventions (Bartz et al., 2010). Thus, it is possible that our synchrony intervention was too short to have a reliable impact on empathic accuracy.

Overall, our study along with previous research, paints a picture where synchrony is not linked with greater accuracy in inferring or sharing others' emotions.

Synchrony and Theory of Mind

Synchronous participants attributed more to mental states to abstract geometrical shapes but not to their partner. Attribution of mental states to the partner was measured using a questionnaire. Attribution of mental states more broadly was tested using a task involving a set of videos of geometrical shapes moving so as to suggest human interaction, in the absence of any contextual verbal or non-verbal cues other than movement. We screened participants' descriptions of these videos for the degree of intentionality they attributed to the shapes and found that this was higher for participants in the synchrony compared to the asynchrony group. This suggests that synchrony has an effect on the attribution of intentionality. This result at first glance may seem to contradict a prior study that found that the quality of synchrony did not correlate with ToM performance (Koehne et al., 2016). In that study, participants, after a unilateral synchronization task, were shown videos of four human characters getting together for a dinner party and then had to respond to questions as to what the different characters were thinking, feeling or intending. The individual differences in scores on this task (Movie for Assessment of Social Cognition, MASC; Dziobek et al., 2006) did not correlate with the accuracy of the synchronization. We argue that this finding does not contradict but complements the present results. The Koehne study assessed the accuracy with which participants can infer other people's mental states which is a different aspect of ToM from what we tested here, namely the extent to which participants spontaneously ascribe mental states independently of whether they do so accurately or not. Thus, a preliminary picture seems to emerge from studies so far on synchrony and ToM and empathy where some subjective measures are affected by synchrony, but no accuracy measures are: no effect on empathic accuracy (our study and Fujiwara and Daibo, 2021), nor emotion sharing (our study), nor reading-the-mind-in-the-eyes (Baimel et al., 2018) nor assessing intentions in a movie (MASC; Koehne et al., 2016).

The Triangle task has been successfully used in studies involving typical adults (Devine and Hughes, 2019; Ceccato et al., 2020) and has shown convergent validity with other ToM tasks (Devine and Hughes, 2019; Lecce et al., 2021). Previous research has suggested that the detection of agency on the basis of motion cues, such as velocity changes and movements that appear interactive, may be a precursor of ToM (Blakemore et al., 2003) and relies on brain areas involved in understanding social information in human motion (Castelli et al., 2002). Given that previous research has shown that performance in the Triangle task is associated with social competence (Ceccato et al., 2020), at least in children, possibly the differences we found in this task in adults could also be relevant for social interactions.

Our results suggest that moving in synchrony has effects on other tasks that no longer involve the person we synchronized with (in our case, the Triangle task). This is analogous to prior work documenting effects of synchrony on prosocial behavior, showing that these effects extend beyond the particular people we synchronize with (Reddish et al., 2013; but see also Cirelli et al., 2014; Cirelli, 2018). However, in the present study, we did not observe an effect of synchrony on mental state attribution for the person synchronized with. This contrasts with results of Baimel et al. (2018) who reported that participants in the synchrony condition were more likely to attribute mental states to their partners than participants in the asynchrony condition. This failure to replicate the prior result could be, we speculate, because the effect of synchrony on ToM is smaller in dyads (as we tested) than in triads (as in Baimel et al., 2018). Indeed, although not addressing mental state attribution, previous literature has indicated that group size may moderate synchrony effects on other measures of social affiliation (prosocial behavior and positive affect): the larger the group, the bigger the effect (Mogan et al., 2017). Extrapolating from these findings, we speculate that in our case, the group size (dyads) may have been too small to yield effects that were observed previously for triads.

Our study taken together with prior work suggests that the link between synchrony and ToM may go both ways. We tested the effect of synchrony on ToM. Prior work has documented the opposite direction: whether pre-existing ToM differences lead to greater synchrony. Novembre et al. (2019) divided participants into high and low empathic perspective taking pairs (based on scores of the *perspective taking* subscale of the Interpersonal Reactivity Index, IRI). Participants in the high empathy group synchronized more accurately in time than participants with low empathy. In another set of studies, Autism Spectrum Disorder (ASD) individuals had lower synchronization performance relative to neurotypical controls (Gowen and Miall, 2007; Fitzpatrick et al., 2013, 2017; Marsh et al., 2013). One possibility is that this synchronization difference is related to the documented difference in mentalizing abilities in ASD individuals. However, other differences between typical and ASD individuals other than mentalizing could explain this effect, such as social perceptual processes (Klin et al., 2002). Taken together, existing literature may suggest a bidirectional relationship between synchrony and ToM, as has been proposed before (Shamay-Tsoory et al., 2019). However, the studies for the two directions of this relationship did not use the same measures of ToM (subjective vs. performance-based) and synchrony (spontaneous vs. imposed). This leaves open the possibility that each direction of the relationship holds only for a specific ToM component considered or on the way that synchrony was manipulated, and thus it would not be fully bidirectional. It would be interesting for future studies to further hash out this relationship between ToM and synchrony by evaluating whether an intervention that increases ToM leads to greater synchrony after relative to the before.

In sum, our findings suggest that synchrony affects the tendency to spontaneously ascribe intentionality to moving geometric shapes but not the self-reported attribution of mental states to the synchronizing partner.

Secondary Findings

Participants in the synchrony and asynchrony conditions together, relative to the small talk condition, showed greater emotional congruence (emotion sharing) for negative emotions. This finding was selective: no differences were found between the synchrony and asynchrony groups, nor differences in empathic accuracy, nor differences for positive emotional congruence. The small talk condition was included as a benchmark of the social effects of a relatively natural, normal interaction. The emotional congruence effect observed can be due to many factors and our data do not allow us to determine which. For instance, the synchrony and asynchrony conditions both involved prescribed periodic movements paced by auditory sounds whereas the small talk condition did not. The small talk condition involved verbal interaction whereas the other conditions did not. Or again, the difference in emotion sharing could be due to the fact that the synchrony and asynchrony conditions both performed the same movement, thus giving rise to a mirroring of sort (even though not necessarily at the same time). The small talk condition allowed for sharing of personal details whereas the synchrony/asynchrony conditions did not. Note also that the small talk conversation could have given rise spontaneously to more or less synchronous movements, as has been previously observed, due to a number of factors (Fusaroli et al., 2013; Varlet et al., 2014; Schmidt and Fitzpatrick, 2019; Fujiwara and Daibo, 2021). Any of these differences, or yet others we have not listed, could be responsible for the emotion sharing difference observed here.

Both empathic accuracy and emotional congruence were greater for negative than for positive emotions. This was true across groups and, thus, not affected by synchrony or small talk. We are not aware of studies systematically investigating whether positive or negative emotions are more prone to be shared. Perhaps what we observed is because negative emotional information tends be more salient (Baumeister et al., 2001; Vaish et al., 2008; Fessler et al., 2015), since individuals in many cases tend to prefer sharing positive emotional content (Gillath et al., 2005). Prior literature has drawn distinctions between empathy for negative and positive emotions (Andreychik and Lewis, 2017). Empathy for others' positive emotions is associated with dispositional positive emotionality (propensity to experience frequent, intense, or enduring positive affect), engagement in behaviors aimed to enhance others' positive emotions and with engaging in random acts of kindness (Andreychik and Migliaccio, 2015). Empathy for others' negative emotions is associated with helping others when it is framed as avoiding them to suffer (Andreychik and Lewis, 2017). Our data does not allow us to distinguish whether greater sharing of negative emotions is a general phenomenon or an artifact of the conversation that we had our participants engage in. In our study, participants always first talked about a negative event, which may have led to a greater overall negative tone to the conversation which was reflected in greater sharing of negative emotions.

Future Directions and Limitations

Synchrony can occur spontaneously or intentionally. When intentional, it may come about through different processes that have different social outcomes. Cacioppo et al. (2014) distinguish between orchestration (when multiple participants follow a common stimulus), unilateral entrainment (when one of the participants is a leader that the others follow) or reciprocal entrainment (when the participants mutually adjust their movements). Although a growing literature documents differences in dynamics between these kinds of synchrony, the social effects of each have received little systematic comparison. The present study focuses on synchronizing with an imposed metronome (i.e., orchestration) as a number of prior studies did (Macrae et al., 2008; Hove and Risen, 2009; Valdesolo and DeSteno, 2011; Reddish et al., 2013, 2016; Baimel et al., 2018). Although this allowed us greater control in terms of tempo over time and across dyads, it leaves open the possibility that social effects would have been different had we studied spontaneous or bilateral entrainment. Future studies could explore these possibilities. At least in principle, it is possible that bidirectional synchrony would have a stronger effect on ToM and empathy than a synchrony condition in which participants are required to synchronize with an external metronome because in that case there is no shared goal. A prior study that focused on social effects other than ToM and empathy indeed found that bidirectional synchronization (shared goal) has larger effects on measures of trust, cooperation and perceived similarity and closeness toward the synchronizing partners than a unilateral synchrony with a metronome (Reddish et al., 2013).

The present study did not include pre-manipulation measures of the variables of interest so we could not control for potential differences in baseline levels of social affiliation, ToM and empathy. Second, we did not measure the fine-grained accuracy of synchronous movements in each pair of participants (e.g., the time differences between the movements of the two partners). This could be helpful in future studies to ask whether pairs who are more accurately synchronous in time also yield greater effects on social affiliation and social cognition. Third, possibly our sample size was too small to detect more subtle effects. Further, the absence of effects on empathic measures (empathic accuracy and emotional congruence) reported here could be due to the online nature of the test. It is possible, at least in principle, that these effects would be observed had participants met in person. We think this possibility is less likely, given the degree of convergence between our result and that of prior studies on other social measures. However, future studies could test this more directly.

Our study was conducted during a time of exceptional social circumstances. In the spring of 2020, as data was collected, our Italian participants were in a state of lockdown where in-person social interactions were in many cases severely limited. In that situation online interactions may have provided the social support that is otherwise obtained in-person meetings (Pancani et al., 2021; Marinucci et al., 2022). This could have biased the results of the present study: perhaps participants were more open to engage in online interpersonal interactions than they would have been under conditions of less social isolation. Note that boosting closeness under these exceptional circumstances also highlights the potential of our intervention: that online encounters can, through even brief periods of synchronous movement, become a source of interpersonal closeness. Closeness, in turn, has been associated with greater emotional wellbeing during the pandemic (Cavallini et al., 2021). In this way, online social interactions may be beneficial when in-person interactions are not available (Waytz and Gray, 2018).

In conclusion, our study found that synchronous movements during online encounters increased a number of measures of social affiliation and Theory of Mind, but not empathic accuracy or emotion sharing. These results highlight the potential of synchronous movement in online encounters to affect a subset of social cognition and affiliation measures.

DATA AVAILABILITY STATEMENT

The datasets supporting the conclusions of this article are publicly available online via https://osf.io/Jchzb/.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Ethics Committee of the Department of Brain and Behavioral Sciences of the University of Pavia. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

Conceptualization and writing: CB, SL, and FV. Investigation and data collection: CB. Supervision: SL and FV. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fpsyg.2022.886639/full#supplementary-material

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