

Research article

Neural multimodal integration underlying synchronization with a co-performer in music: Influences of motor expertise and visual information



Renee Timmers^{a,*}, Jennifer MacRitchie^b, Siobhan M. Schabrun^c, Tribikram Thapa^c, Manuel Varlet^{b,d}, Peter E. Keller^b

^a Department of Music, The University of Sheffield, 34 Leavygreave Road, Sheffield, S3 7RD, UK

^b MARCS Institute for Brain, Behaviour and Development, Western Sydney University, Locked Bag 1797, Penrith, NSW, 2751, Australia

^c Brain Rehabilitation and Neuroplasticity Unit, Western Sydney University, Locked Bag 1797, Penrith, NSW, 2751, Australia

^d School of Psychology, Western Sydney University, Locked Bag 1797, Penrith, NSW, 2751, Australia

ARTICLE INFO

Keywords:

Synchronization
Motor expertise
Dorsal premotor cortex
Intraparietal sulcus
Sensorimotor integration
Music performance
Visual information

ABSTRACT

Sensorimotor synchronization is a general skill that musicians have developed to the highest levels of performance, including synchronization in timing and articulation. This study investigated neurocognitive processes that enable such high levels of performance, specifically testing the relevance of 1) motor resonance and sharing high levels of motor expertise with the co-performer, and 2) the role of visual information in addition to auditory information. Musicians with varying levels of piano expertise (including non-pianists) performed on a single piano key with their right hand along with recordings of a pianist who performed simple melodies with the left hand, synchronizing timing and articulation. The prerecorded performances were presented as audio-only, audio-video, or audio-animation stimuli. Double pulse Transcranial Magnetic Stimulation (dTMS) was applied to test the contribution of the right dorsal premotor cortex (dPMC), an area implicated in motor resonance with observed (left-hand) actions, and the contribution of the right intraparietal sulcus (IPS), an area known for multisensory binding. Results showed effects of dTMS in the conditions that included visual information. IPS stimulation improved synchronization, although this effect was found to reverse in the video condition with higher levels of piano expertise. dPMC stimulation improved or worsened synchronization ability. Level of piano expertise was found to influence this direction in the video condition. These results indicate that high levels of relevant motor expertise are required to beneficially employ visual and motor information of a co-performer for sensorimotor synchronization, which may qualify the effects of dPMC and IPS involvement.

1. Introduction

Research on sensorimotor synchronization has uncovered cognitive processes that allow performers to coordinate with high temporal precision. This work highlights the role of allocating attention to self and others [1], predicting the timing of co-performers [2], and reactively correcting for discrepancies in interpersonal timing [3]. Notably, successful temporal coordination between performers can be realized on the basis of auditory information only (e.g. [3,4]). Seeing the co-performer in addition to hearing them may under certain circumstances decrease synchronization precision [2]. Nevertheless, in natural contexts, performers use both visual and auditory information to guide coordination with co-performers [5,6]. This raises the question of how vision is employed, and how it is integrated with auditory cues and the

planning of motor actions to contribute to precise temporal coordination.

The visual channel provides a rich source of information about body movements, cuing observers about ongoing actions and action intentions (e.g. [7]). Previous studies have shown the relevance of the observer's motor repertoire for perceptual sensitivity to visually observed actions [6]. Indeed, motor resonance to observed actions may contribute causally to improved temporal synchronization in particular when the performer has practiced the co-performers' music [8,9].

Evidence for the beneficial role of motor resonance for synchronization comes from studies that employed double pulse Transcranial Magnetic Stimulation (dTMS) to temporarily inhibit the involvement of brain areas related to simulating others' actions. dTMS applied to the primary motor cortex reduced accurate adjustment to a tempo-change

* Corresponding author.

E-mail addresses: r.timmers@sheffield.ac.uk (R. Timmers), j.macritchie@westernsydney.edu.au (J. MacRitchie), s.schabrun@neura.edu.au (S.M. Schabrun), tribikram.thapa@monash.edu (T. Thapa), m.varlet@westernsydney.edu.au (M. Varlet), p.keller@westernsydney.edu.au (P.E. Keller).

<https://doi.org/10.1016/j.neulet.2020.134803>

Received 6 November 2019; Received in revised form 20 January 2020; Accepted 30 January 2020

Available online 31 January 2020

0304-3940/© 2020 Elsevier B.V. All rights reserved.

in auditory stimuli [9], while dTMS applied to the dorsal premotor cortex (dPMC) reduced synchronization in a turn-taking task that presented visual and auditory information of a co-performer [8]. Participants performed their part with the right hand, while the pre-recorded pianists performed with their left hand. Motor areas in the right hemisphere were stimulated to target simulations of left-hand co-performer actions rather than interfering with right hand actions.

The present study aimed to investigate the relevance of visual information for motor simulation, and the influence of instrumental expertise, hypothesizing that both strengthen the role of dPMC. Furthermore, we aimed to examine the role of multisensory binding by including dTMS application to the right intraparietal sulcus (IPS, as in [10] and [11]). We hypothesized that cross-modal binding is necessary for visual information to (positively or negatively) influence temporal synchronization and therefore predicted that the application of dTMS to IPS may causally affect synchronization accuracy.

These aims led to a study design that combined three audio-visual conditions – audio-only, audio-video, and audio-animation – with three TMS conditions – Sham, dPMC, and IPS, and one between-participant variable of piano expertise, including non-pianists. The effect of dTMS on synchronization ability was tested for each type of audio-visual stimuli, using three measures of “asynchronization”. A basic musical synchronization task was used without tempo changes or turn-taking requirements. The audio-animation condition was included to examine the relevance of full video information for action simulation and cross-modal binding, or the sufficiency of movement cues.

2. Materials and methods¹

2.1. Participants

Twenty-six musically trained participants took part in the study.² Two were left handed, and the others right handed. All had normal hearing and normal or corrected-to-normal vision. TMS safety screening was applied to exclude individuals with a history of epilepsy, neurological or musculoskeletal conditions. Participants were grouped into non-pianists, amateur pianists, semi-professional pianists, and professional pianists based on self-report (Table 1), which was preferred over years of experience to avoid influences of age and include differences in level of engagement and proficiency.

The study received ethical approval from University of Western Sydney Human Research Ethics Committee (H9990). Participants gave informed consent and were free to withdraw at any time. None of the participants wished to do so. They received a small fee for participation.

2.2. Material

An accomplished pianist (serious amateur) performed the left-hand part of four beginner-level melodies (see Fig. 1).

The pianist played on a Yamaha Clavinova. MIDI³ recordings were made to assess note onset and offset timing. Audio and video recordings were made for presentation to participants.

Video recordings were taken from the side, focusing on the left lower arm and hand. To create videos for the audio-animation condition, a green dot was painted on the pianist’s hand, and changes in the position of the dot across video samples were tracked using computer vision techniques in a two-dimensional space. Animations were generated that showed the movement of the green dot on top of a flesh-colored rectangle within a black background (see Fig. 2).

The pianist performed the music with some expressive variation in timing and dynamics to create naturalistic stimuli. Three performances were included of each melody. The overall articulation was staccato, the intensity was *forte* (loud) or *mezzo forte* (moderately loud), average tempo ranged between 183–203 BPM and included a modest degree of tempo rubato of on average 7.8 % of the average note duration. Half note inter-onset-intervals (IOIs) were on average 624 ms (comparable to IOIs in 8 and 9).

2.3. Procedure

2.3.1. Musical preparation

Participants were sent instruction videos at least two weeks before participation to familiarize themselves with the left-hand melodies of the musical stimuli by actively practicing them. Previous studies have shown the benefit of having practiced the other’s part for synchronization and motor simulation [8,9]. Video instructions included sound and showed which key to press with what finger at what time in a steady tempo (140 BPM).

Participant’s familiarity with the melodies was assessed before participation in the experimental trials. Further practice was given, until the participant performed the melodies without hesitation and errors.

2.3.2. TMS preparation and procedure⁴

Single pulse TMS induced muscle activation in the left hand was measured using electromyography to determine the optimal site for M1 stimulation (hotspot) and resting motor threshold. A standard 70 mm figure-of-eight TMS coil was positioned with the handle pointing postero-laterally at a 45° angle to the sagittal plane. The coil was moved until largest muscle responsiveness was found. Resting motor threshold was subsequently defined as the minimal TMS intensity required to elicit a muscle response of 0.05 mV peak-to-peak amplitude in 5 out of 10 trials.

For the experimental trials, double pulse TMS (dTMS) at 120 % resting motor threshold was delivered to P4⁵ as a proxy for stimulation of the right IPS [10], to the right dPMC (3 cm anterior to the hot-spot, as in 8), or at 90° coil orientation to Cz for Sham stimulation. This method of localizing dPMC targets a rostral part of dPMC [12].

dTMS was triggered at three score-positions, distributed across two repeats to assure a minimum of 6 s between stimulations. In one trial, pulses were triggered at target notes T1 and T3, and, in the other trial, at target note T2 (Fig. 1). The first pulse of dTMS was delivered 100 ms before the second, which coincided with the target note onset.⁶

2.3.3. Procedure of experimental trials

Participants played along with the presented performances on a silent Yamaha Clavinova with one finger of their right hand. Their task was to synchronize with the “virtual co-performer” as precisely as possible, playing the same rhythm, articulation and dynamics. A computer screen on top of the piano displayed the visual information and audio was presented over speakers. Onset and offset timing of key presses were recorded using MIDI.

A blocked procedure was used in which two melodies were performed in one block and two melodies in the second block. Each block contained all conditions: 2 melodies were presented 6 times (two repetitions of three performances) in each audio-visual condition. This was repeated for each TMS condition. The order of TMS and audio-visual conditions was reversed in the second block of a participant, counter-balancing the orders within participants. Orders were also

¹ See Supplementary material for methodological details.

² A sample size of 26 was deemed sufficient on the basis of samples of 10 and 15 participants in closely related studies [9,8].

³ Musical Instrument Digital Interface (MIDI) instruments record onset and offset timing and key velocity for each performed note.

⁴ See Supplementary material for further details.

⁵ An adjustable EEG cap was used to determine the location of P4.

⁶ This was the middle condition in [8], who found no significant difference depending on temporal placement.

Table 1

Participant characteristics according to level of piano expertise based on main instrument and self-defined level of musicianship.

Level of piano expertise	Main instrument	Number of participants (female)	Median age (and range) in years	Median (and range) of years of playing an instrument
(3) Professional	Piano	8 (7)	32 (20–44)	27 (15–38)
(2) Semi-professional	Piano	8 (4)	22.5 (18–37)	16 (10–33)
(1) (Serious) amateur	Piano	5 (3)	21 (18–23, 62*)	15 (8–17, 54*)
(0) Non-pianist	Other than piano	5 (2)	25 (22–41)	20 (10–31)

* One data point for age and years of playing an instrument is an outlier and listed separately. All participants were included in the analyses.



Fig. 1. Left hand part of melodies from Bela Bartok's Microcosmos I. Recorded performances of these melodies were used as stimuli. T1-3 indicate target notes for DTMS stimulation.

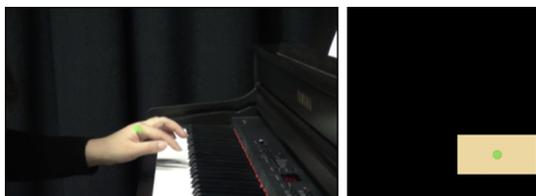


Fig. 2. Illustration of the video and animation stimuli.

varied across participants. The total duration of an experimental session was around 90 min, including a break between blocks.

2.3.4. Data processing

Data analysis focused on the timing of target notes. Differences between the pre-recorded and participants' performances were measured with respect to the target note's onset timing, duration (note onset to note offset), and the time interval to the next note (IOI). Differences greater than 500 ms were left out, as they were likely the result of an error (e.g. missing note). The distribution of the remaining data was checked for outliers, replacing outliers with the mean plus or minus 2.5 standard deviations. This concerned less than 0.03 % for timing, 1.44 % for IOI, and 2 % for duration difference data. The resulting data set confirmed the assumptions of normally distributed data. Some participants had missing data for short notes. This concerned two participants of the amateur piano group, two participants of the semi-professional piano group and one participant of the professional piano group, leading to reduced degrees of freedom for some of the analyses.

2.3.5. Synchronization measures (*sdONSET*, *sdIOI*, *sdDUR*)

The standard deviations (SD) of the differences in onset-timing

(*sdONSET*), IOI (*sdIOI*), and duration (*sdDUR*) were used as summary measures of performance across trials in each condition. The SD captures the variability with which a participant aligned in time with the pre-recorded performance. Separate estimates were made for long and short target notes and for each TMS and AV condition. The standard deviation of timing differences (generally applied to onset or IOI) or "asynchronization" [13] captures the lack of consistency with which performers synchronize. It is in line with well-established timing models that expect asynchrony correction to minimize asynchrony variance [3,14].

Whilst differences in IOI and onset timing are typically used to investigate synchronization [3,13], the inclusion of a measure related to duration is uncommon. It was included to reflect the musical task: to truly perform together, musicians align both onset timing and articulation (as discussed in [15]).

2.3.6. Data analysis

Analysis of Variance (ANOVA) was used to test the effects of TMS stimulation (TMS) and piano expertise (Piano) on the three dependent variables (*sdONSET*, *sdIOI* and *sdDUR*). The ANOVAs were conducted separately for each type of audio-visual stimuli. Note duration (NDUR, 2 levels, short and long) was included as a within-participants independent variable for analysis related to the musical stimuli.

3. Results

Table 2 shows the main results of the ANOVA for each dependent variable and each type of audio-visual stimuli. Results will be discussed per audio-visual stimulus type.

Table 2

Results of the univariate ANOVAs testing the effects of TMS, NDUR and Piano on sdONSET, sdIOI, and sdDUR for audio-only (top), audio-video (middle) and audio-animation stimuli (bottom). Significant effects are highlighted in bold.

	df [†]	sdONSET		sdIOI		sdDUR	
		F	r	F	r	F	r
<i>Audio-only</i>							
TMS	2, 38	0.055	.055	0.664	.184	0.366	.138
TMS*Piano	2, 38	0.688	.187	1.412	.263	0.434	.148
NDUR	1, 19	1.964	.307	38.127***	.817	67.374***	.883
NDUR*Piano	1, 19	1.137	.237	10.503**	.597	3.322	.386
TMS*NDUR	2, 38	0.071	.063	0.415	.145	0.431	.148
TMS*NDUR*Piano	2, 38	0.107	.077	0.043	.045	2.642	.349
Piano	1, 19	0.243	.114	5.678*	.480	0.101	.071
<i>Audio-video</i>							
TMS	2, 38	0.602	.176	1.657	.283	4.125*	.422
TMS*Piano	2, 38	0.995	.224	1.638	.281	4.010*	.417
NDUR	1, 19	0.020	.032	28.552***	.775	110.091***	.924
NDUR*Piano	1, 19	0.494	.158	6.026*	.491	2.717	.354
TMS*NDUR	2, 38	0.166	.095	0.252	.114	0.079	.063
TMS*NDUR*Piano	2, 38	1.437	.265	0.124	.084	0.030	.045
Piano	1, 19	4.435*	.435	3.179	.378	1.115	.235
<i>Audio-animation</i>							
TMS	2, 38	4.092*	.421	4.534*	.434	1.755	.291
TMS*Piano	2, 38	2.168	.319	0.571	.170	1.044	.228
NDUR	1, 19	3.020	.370	23.638***	.744	69.889***	.887
NDUR*Piano	1, 19	0.014	.032	3.006	.370	2.104	.316
TMS*NDUR	2, 38	2.964	.367	1.958	.305	0.230	.110
TMS*NDUR*Piano	2, 38	1.414	.263	0.617	.176	0.395	.141
Piano	1, 19	4.898*	.453	13.845**	.650	5.773*	.483

[†] Degrees of freedom are corrected for violations of sphericity where appropriate.

* $p < .05$.

** $p < .01$.

*** $p < .001$.

3.1. Audio-only

For the audio-only conditions, no significant effect of TMS or interactions with TMS were found on any of the dependent variables (see Fig. 3 for means and SE per condition). The main effect of NDUR was significant for sdIOI ($p < .001$) and sdDUR ($p < .001$), as was the interaction between NDUR and Piano for sdIOI ($p = .004$), and the main effect of Piano on sdIOI ($p = .028$). The effects were as expected: asynchronization was larger for long notes than short notes (IOI: $M = 38.869$, $SE = 1.701$ vs. $M = 24.924$, $SE = 1.625$; DUR: $M = 63.728$, $SE = 2.430$ vs. $M = 29.768$, $SE = 2.009$). Furthermore, IOI asynchronization decreased with increasing levels of piano expertise ($r = -.480$, $p = .028$, $df = 20$). The interaction between NDUR and Piano was related to a negative correlation between Piano and sdIOI for long notes ($r = -.663$, $p = .001$, $df = 20$), but no reliable correlation for short notes ($r = .098$, $p = .673$, $df = 20$).

3.2. Audio-video

For the audio-video conditions, a significant main effect of TMS was found on sdDUR ($p = .024$), and an interaction between TMS and Piano for sdDUR ($p = .026$). This main effect of TMS is illustrated in Fig. 3: DUR asynchronization was smallest under IPS stimulation and highest under Sham stimulation. Planned contrasts confirmed significant differences between Sham and dPMC stimulation ($p = .044$), and between Sham and IPS stimulation ($p = .014$).

To investigate the interaction between TMS and Piano on sdDUR, level of piano expertise of individuals was correlated with differences in sdDUR between TMS conditions, which highlights how the effect of TMS (differences between conditions) varies with piano expertise. This analysis showed positive correlations with the difference between dPMC and Sham ($r = .481$, $p = .027$, $df = 20$) and with the difference between IPS and Sham ($r = .436$, $p = .048$, $df = 20$). These positive correlations relate to changes in the effect of dPMC and IPS stimulation

with greater levels of piano expertise, from a decrease in DUR asynchronization ($\Delta M < 0$, for expertise levels 0 and 1 under dPMC stimulation; and levels 0, 1, and 2 under IPS stimulation) to an increase ($\Delta M > 0$, for expertise levels 2 and 3 under dPMC stimulation, and level 3 under IPS stimulation)⁷.

The main effect of NDUR was significant for sdIOI ($p < .001$) and sdDUR ($p < .001$), the interaction between NDUR and Piano for sdDUR ($p = .024$), and the main effect of Piano on sdONSET ($p = .049$). The effects of NDUR and Piano were as previously observed: asynchronization was larger for long notes than short notes (sdIOI: $M = 37.644$, $SE = 1.910$ vs. $M = 23.999$, $SE = 1.148$; sdDUR: $M = 61.028$, $SE = 2.244$ vs. $M = 28.676$, $SE = 0.976$). The interaction between NDUR and Piano was such that a negative association between Piano and sdIOI was found for long notes ($r = -.496$, $p = .022$, $df = 20$, but not for short notes ($r = .198$, $p = .389$, $df = 20$). A negative association was present between Piano and sdONSET ($r = -.435$, $p = .049$, $df = 20$), indicating improved performance with higher levels of piano expertise.

3.3. Audio-animation

For the audio-animation conditions, a significant main effect of TMS was found for sdONSET ($p = .025$) and sdIOI ($p = .017$). This effect of TMS showed the same pattern for both measures: asynchronization was relatively large under dPMC stimulation and relatively small under IPS stimulation. Planned contrasts indicated that the pair-wise comparisons with Sham stimulation failed to reach significance for sdONSET ($p = .268$ for dPMC; $p = .320$ for IPS). For sdIOI, the difference between Sham and IPS was significant ($p = .044$), but not the difference between Sham and dPMC ($p = .052$). As can be seen in Fig. 3, the main contrast was between asynchronization under dPMC and IPS stimulation.

⁷ Scatterplots are provided in the Supplementary material.

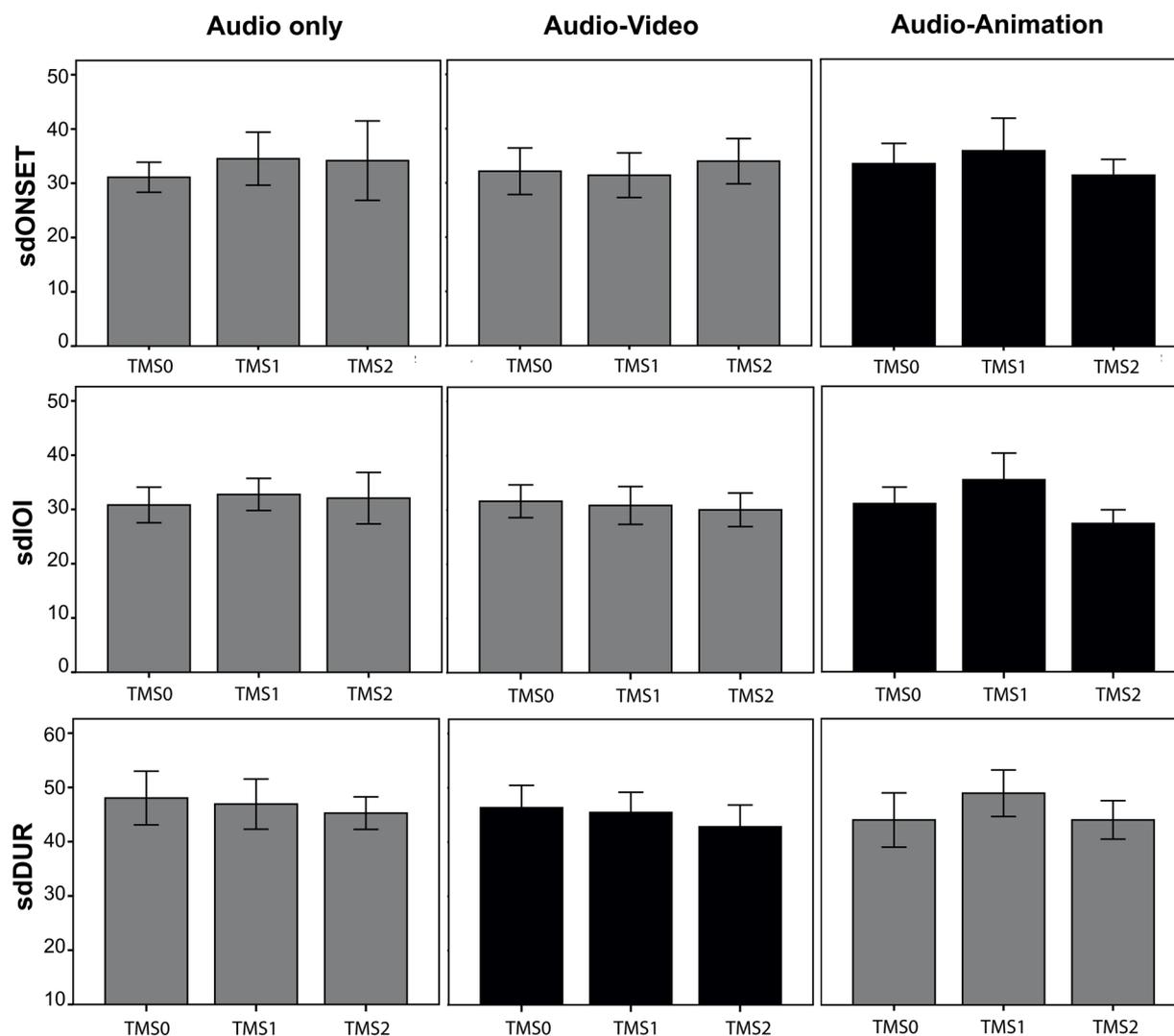


Fig. 3. Mean and SE of each asynchronization measure by TMS and audio-visual condition. Significant effects of TMS are in black. Non-significant differences are grey. dTMS conditions include Sham (TMS0), dPMC (TMS1) and IPS (TMS2).

Main effects were found of NDUR on sdIOI ($p < .001$) and sdDUR ($p < .001$), which were again related to larger asynchronization for long notes than short notes (sdIOI: $M = 38.704$, $SE = 1.677$ vs. $M = 23.769$, $SE = 1.589$; sdDUR: $M = 63.221$, $SE = 2.400$ vs. $M = 28.090$, $SE = 1.739$). Main effects of Piano were observed for sdONSET, sdIOI, and sdDUR. These consisted of significant negative correlations between Piano and sdONSET ($r = -.453$, $p = .039$, $df = 20$), Piano and sdIOI ($r = -.649$, $p = .001$, $df = 20$), and Piano and sdDUR ($r = -.483$, $p = .027$, $df = 20$).

3.4. Testing absolute differences in timing and duration

Previous research that is closely related to this study [8] examined synchronization accuracy by measuring the absolute difference in onset timing rather than taking the standard deviation of these differences. The benefit of using asynchronization based on the standard deviation is that it measures accuracy irrespective of the general tendency of a performer to anticipate or lag, or to play more or less legato. Nevertheless, to examine the generalizability of our results to this measure of asynchrony, the analyses were repeated for the absolute differences in onset-timing, IOI and duration, which were log-transformed to correct for positive skew. These analyses showed a significant interaction between TMS and Piano in the video conditions for IOI ($F(2,44) = 3.872$, $p = .028$, $r = .387$). This interaction was examined by correlating the

differences between TMS conditions with piano expertise, showing a positive correlation for differences in means under IPS compared to Sham stimulation ($r = .466$; $p = .022$, $df = 23$). With greater piano expertise, stimulation of IPS led to larger asynchrony ($\Delta M > 0$ for levels 1, 2 and 3) rather than smaller ($\Delta M < 0$ for level 0). The positive correlation with differences in means under dPMC and Sham stimulation was not significant ($r = .346$; $p = .098$, $df = 23$).⁸

4. Discussion

The asynchronization measures provided converging evidence for a significant effect of dTMS application to dPMC and IPS compared to Sham on musical synchronization, specifically if visual information was present. Furthermore, there was evidence for the effect of dTMS to vary with piano expertise.

The effect of dTMS application to dPMC for the audio-animation condition was as previously found: interference with motor simulation reduces the ability to precisely synchronize with a recorded co-performer [8]. In the audio-video condition, stimulation of dPMC was in contrast found to improve synchronization (decrease in sdDUR). This effect was however dependent on level of piano-expertise: with greater

⁸ Scatterplots are provided in the Supplementary material.

expertise the effect reversed and dPMC stimulation increased DUR asynchronization.

The main effect of dTMS application to IPS was a reduction in ONSET and IOI asynchronization in the audio-animation condition. However, within the audio-video condition, this effect interacted with piano expertise for DUR asynchronization, which was also found for IOI in the audio-video condition for the alternative synchronization measure. With greater piano expertise, an increase in asynchronization was observed rather than a decrease.

The main effect of a reduction of asynchronization in the context of IPS and dPMC stimulation requires further explanation. We interpret the reduction as related to an increased complexity of the task with the addition of visual information and motor resonance, which leads to an increase in timing variation. The interaction with piano expertise shows that beneficial employment of visual information for synchronization requires high levels of relevant motor expertise, as also indicated by the multiple significant correlations with expertise for conditions including visual stimuli. Effective use of visual information may involve its use as a source for action simulation [9], and in making inferences about the co-performer's action goals, as in other forms of joint action [16]. Notably, the animation condition seemed to be a source for action simulation as much as for visual cuing, given the significant effect of dPMC stimulation, indicating that reduced animations of biological motion provide rich sources of information that can be comparable with full video presentations [17]. Future research may reduce the salience of the auditory cues for synchronization, which would allow for more specific testing of the ability to rely on visual information. Furthermore, it will be important to replicate the investigation with a balanced group of expert pianists and non-pianists, as the non-pianist group was small in our sample.

The three asynchronization measures showed varied but not contradictory results. We interpret this finding as an indication that similar processes shape sensorimotor synchronization in terms of onset timing, tempo (IOI), and articulation. It will be of interest to investigate this systematically by isolating instructions to either include onset timing, tempo variation or articulation, thereby controlling the focus of participants' attention to specific performance aspects, which may also reduce inter- and intra-individual variation in the data.

To conclude, the results of this study are consistent with a causal role of both the intraparietal sulcus and the dorsal premotor cortex in synchronization with a musical co-performer. The findings further indicate a change with expertise in the neurocognitive processes involved in interpersonal synchronization, with greater relevant expertise enhancing the ability to beneficially employ visual and motor information generated by a co-performer.

Credit author statement

RT was responsible for design, data collection, analysis, and write up. JM, MV and PK advised on the design of the study, experimental procedures and manner of data collection and analysis. JM was responsible for stimuli presentation and data recording, including creating the animations. SS and TT advised on and assisted with TMS procedures. TT assisted with data collection. All co-authors provided feedback and input on revisions of the manuscript.

Declaration of Competing Interest

None.

Acknowledgements

This research was supported by a Leverhulme International Academic Fellowship to RT (IAF-2015-013) and a Future Fellowship grant, Australian Research Council to PK (FT140101162).

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.neulet.2020.134803>. Data files can be found at doi: [10.15131/shef.data.11791521](https://doi.org/10.15131/shef.data.11791521).

References

- [1] P.E. Keller, Attentional resource allocation in musical ensemble performance, *Psychol. Music* 29 (2001) 20–38.
- [2] P.E. Keller, M. Appel, Individual differences, auditory imagery, and the coordination of body movements and sounds in musical ensembles, *Music Percept.* 28 (2010) 27–46.
- [3] B.H. Repp, Sensorimotor synchronization: a review of the tapping literature, *Psychon. Bull. Rev.* 12 (2005) 969–992.
- [4] W. Goebel, C. Palmer, Synchronization of timing and motion among performing musicians, *Music Percept.* 26 (2009) 427–438.
- [5] L. Bishop, W. Goebel, When they listen and when they watch: pianists' use of non-verbal audio and visual cues during duet performance, *Musicae Sci.* 19 (2015) 84–110.
- [6] C. Wöllner, R. Cañal-Bruland, Keeping an eye on the violinist: motor experts show superior timing consistency in a visual perception task, *Psychol. Res.* 74 (2010) 579–585.
- [7] H. Bekkering, S.F. Neggers, Visual search is modulated by action intentions, *Psychol. Sci.* 13 (2002) 370–374.
- [8] L.V. Hadley, G. Novembre, P.E. Keller, M.J. Pickering, Causal role of motor simulation in turn-taking behavior, *J. Neurosci.* 35 (50) (2015) 16516–16520.
- [9] G. Novembre, L.F. Ticini, S. Schütz-Bosbach, P.E. Keller, Motor simulation and the coordination of self and other in real-time joint action, *Soc. Cognit. Affect. Neurosci.* 9 (2014) 1062–1068.
- [10] N. Bien, S. ten Oever, R. Goebel, A.T. Sack, The sound of size: crossmodal binding in pitch-size synesthesia: a combined TMS, EEG and psychophysics study, *Neuroimage* 59 (2012) 663–672.
- [11] S. Pasalar, T. Ro, M.S. Beauchamp, TMS of posterior parietal cortex disrupts visual tactile multisensory integration, *Eur. J. Neurosci.* 31 (2010) 1783–1790.
- [12] H.R. Siebner, S.R. Filipovic, J.B. Rowe, C. Cordivari, W. Gerschlagler, J.C. Rothwell, R.S. Frackowiak, K.P. Bhatia, Patients with focal arm dystonia have increased sensitivity to slow-frequency repetitive TMS of the dorsal premotor cortex, *Brain* 126 (2003) 2710–2725.
- [13] R.A. Rasch, Timing and synchronization in ensemble performance, in: J.A. Sloboda (Ed.), *Generative Processes in Music: The Psychology of Performance, Improvisation, and Composition*, Clarendon Press, Oxford, 1988, pp. 70–90.
- [14] D. Vorberg, H.H. Schulze, Linear phase-correction in synchronization: predictions, parameter estimation, and simulations, *J. Math. Psychol.* 46 (2002) 56–87.
- [15] P.E. Keller, Ensemble performance: interpersonal alignment of musical expression, in: D. Fabian, R. Timmers, E. Schubert (Eds.), *Expressiveness in Music Performance: Empirical Approaches Across Styles and Cultures*, Oxford University Press, Oxford, 2014, pp. 260–282.
- [16] L.M. Satcheli, G. Tieri, S.M. Aglioti, M. Candidi, Transitory inhibition of the left anterior intraparietal sulcus impairs joint actions: a continuous theta-burst stimulation study, *J. Cognit. Neurosci.* 30 (2018) 737–751.
- [17] R. Blake, M. Shiffrar, Perception of human motion, *Annu. Rev. Psychol.* 58 (2007) 47–73.