

RESEARCH ARTICLE

Upper rate limits for one-to-one auditory–motor coordination involving whole-body oscillation: a study of street dancers and non-dancers

Akito Miura^{1,*}, Shinya Fujii², Masahiro Okano³, Kazutoshi Kudo^{1,4} and Kimitaka Nakazawa¹**ABSTRACT**

The capacity for auditory–motor coordination (AMC) is shared by several species, among which humans are most flexible in coordinating with tempo changes. We investigated how humans lose this tempo flexibility at their upper rate limit, and the effect of skill level on this phenomenon. Seven skilled street dancers, including a world champion, and 10 non-dancers were instructed to bend their knees according to a metronome beat in a standing position at eight constant beat frequencies (3.8–5 Hz). Although maximum frequency of movement during the task was 4.8 Hz in the non-dancers and 5.0 Hz in the dancers, the rate limit for AMC was 4.1 Hz in the non-dancers and 4.9 Hz in the dancers. These results suggest that the loss of AMC was not due to rate limit of movement execution but rather to a constraint on the AMC process. In addition, mediation analysis revealed that a kinematic bias (i.e. the extent of knee flexion during the task) causally affected the extent of phase wandering via mediating factors (e.g. the extent to which movement frequency was reduced relative to the beat frequency). These results add evidence that gravity acts as constraint on AMC involving vertical rhythmic movement.

KEY WORDS: Maximum frequency, Sensorimotor synchronisation, Vertical rhythmic movement, Gravity, Dance

INTRODUCTION

Auditory–motor coordination (AMC) is the coordination of a rhythmic movement with a rhythmic auditory sequence, and is typically seen in dance and musical performance. For example, we rhythmically bend our knees when listening to a musical beat in a dance club. As our ancestors have enjoyed dance and music since prehistory, AMC is ubiquitous in human societies (McNeill, 1997). Even young infants show precursors of dancing and singing, suggesting that our brains are primed with AMC capabilities (Fujii et al., 2014; Zentner and Eerola, 2010). There has been increasing interest in how our AMC capabilities emerged through the course of evolution. Recently, evidence has been reported that the capacity for AMC is shared by several other species, such as cockatoos (Patel et al., 2009), parrots (Schachner et al., 2009), budgerigars

(Hasegawa et al., 2011), chimpanzees (Hattori et al., 2013), sea lions (Cook et al., 2013) and possibly horses (Bregman et al., 2013). Comparing the AMC-related characteristics of humans and those of these non-human animals, and finding commonalities and differences among them, provides clues for a theory of the evolution of this ability (for a review, see Honing et al., 2015) and highlights the uniqueness of AMC in humans (Patel, 2014).

In AMC exhibited by humans, the coupling between rhythmic movement and the auditory sequence has been reported to be strong. For example, movement rhythm entrains to an auditory sequence irrespective of intention (Carroll et al., 2001; Miura et al., 2013a, 2011), and rhythmic auditory beats have been reported to stabilise oscillatory human movements; this is known as an anchoring effect (Byblow et al., 1994; Fink et al., 2000; Kudo et al., 2006). Humans show these strong couplings between movement and auditory sequences for the widest range of frequencies among all animals that are reported to possess AMC capabilities; this capacity is called humans' 'tempo flexibility' (Patel, 2014). Outside the tempo range where humans have this tempo flexibility, the coupling between movement and auditory sequence becomes weak, and loss of AMC occurs (Repp, 2006). Imagine a situation in which someone claps along with a metronome: he/she can successfully coordinate the necessary movements with the beat when the tempo is moderate, but when the tempo is very high, he/she can no longer do so. The fastest rate of a pacing sequence at which one can maintain the AMC is referred to as one's upper rate limit (Repp, 2006). A primary focus of this study is how the loss of AMC in humans emerges around the upper rate limit in rapid rhythmic AMC. This is of importance for cross-species AMC research, because it enables us to investigate some commonalities in the loss of AMC between humans and non-human animals that do not possess tempo flexibility.

Here, we investigated AMC at the upper rate limit using whole-body oscillation to the auditory sequence that is typically used in street dance (Miura et al., 2013a,b, 2011, 2014). There are two reasons for this choice of task in terms of cross-species comparison of AMC capability. First, it is still debated whether it is valid to compare different behaviours in different species. Some researchers question cross-species comparison of AMC involving a motor behaviour that is fine tuned (i.e. natural) for some species but not (i.e. is unnatural) for others (for reviews, see Hoeschele et al., 2015; Wilson and Cook, 2016). Human AMC research, including the topic of rate limit, has been conducted mainly using a finger oscillation task (for reviews, see Repp, 2005, 2006). Thus, when biologists compare the characteristics of AMC in humans and non-human animals, the findings based on finger oscillation, which is considered to be representative of human AMC, are compared with AMC findings in other animals. However, whether or not the characteristics of human AMC in the finger oscillation task can be generalised to AMC involving other body parts remains an open

¹Department of Life Sciences, Graduate School of Arts and Sciences, The University of Tokyo, Tokyo 153-8902, Japan. ²Faculty of Environment and Information Studies, Keio University, Kanagawa 252-0882, Japan. ³Ritsumeikan Global Innovation Research Organization, Ritsumeikan University, Shiga 525-0058, Japan. ⁴Graduate School of Interdisciplinary Information Studies, The University of Tokyo, Tokyo 113-0033, Japan.

*Author for correspondence (akito.miura@gmail.com)

© A.M., 0000-0003-1199-9940; S.F., 0000-0001-5003-2367; M.O., 0000-0002-3850-5456; K.K., 0000-0002-3199-9449

question. For cross-species comparison, comparison of AMC using morphologically similar movement seems natural, because the generalisability of AMC characteristics across body parts is not substantiated. In particular, special attention should be paid to cross-species comparison with human hand movement, because of its notable dexterity, which is associated with the evolution of the brain through tool use (Stout and Chaminade, 2012). For example, for cross-species comparison of AMC capabilities between humans and other animals, it seems reasonable to compare whole-body oscillation of humans (Miura et al., 2013a, 2011) with that of cockatoos (Patel et al., 2009), to compare finger oscillation of humans (for a review, see Repp, 2005) with that of chimpanzees (Hattori et al., 2013), and to compare locomotion of humans (Bood et al., 2013) with that of horses (Bregman et al., 2013).

The second reason for the use of this whole-body, dance-like AMC task is that it enabled us to investigate the effect of skill level on AMC, by comparing street dancers and novices (Miura et al., 2013a,b, 2011). Dancers and musicians train to increase their upper rate limit, because loss of coordination significantly impairs the quality of their performance. A comparison between highly trained individuals and novices leads to suggestions for a neurophysiological substrate that underlies high performance on this measure (Nakata et al., 2010). In fact, non-human animals with AMC capabilities are usually highly trained by the experimenter. Findings from highly trained human individuals would have implications for training of AMC in non-human animals. For this study, we were able to recruit a world champion of street dance, which enabled us to investigate highly trained AMC capability.

The loss of 1:1 AMC at the upper rate limit has been investigated by examining the emergence of phase wandering, in which oscillator frequencies become detuned and the phases drift. Previous studies have assumed that there are at least two types of upper rate limit in rapid rhythmic AMC: (1) a biomechanical (motor) rate limit and (2) a perceptual rate limit (for a review, see Repp, 2006). The biomechanical rate limit refers to the maximum frequency at which a motor effector can oscillate. In the case of finger tapping, the biomechanical rate limit is typically between 5 and 7 Hz, corresponding to inter-tap intervals of 150–200 ms. The perceptual rate limit refers to the rate at which one can no longer perceive the timing of a rhythmic auditory sequence correctly. When a person is asked to tap with a metronome every 2 or 4 beats, loss of AMC happens above a beat frequency of 8–10 Hz (Repp, 2006). Because the frequency of tapping is lower than the biomechanical rate limit in this situation, the rate limit of 8–10 Hz is regarded as perceptual in nature. Usually, the upper rate limit of 1:1 AMC tends to be regarded as occurring at the bottleneck of the biomechanical and perceptual rate limits. That is, it is attributed to the biomechanical rate limit, because this is lower than perceptual rate limit (Repp, 2006). We hypothesize, however, another possibility: that the upper rate limit of AMC can be attributed to neither the biomechanical nor the perceptual rate limit, but to a third rate limit. For instance, Kelso et al. (1990) reported that phase wandering in finger-to-beat coordination occurred at below 3.5 Hz, which is far lower than both the associated biomechanical and perceptual rate limits. This suggests that some processes involved in AMC also act as a constraint on the upper rate limit of 1:1 AMC. We term this third kind of rate limit the coordination rate limit.

Miura et al. (2013a) reported that both novices and skilled street dancers could perform 1:1 AMC with whole-body oscillation in stance (i.e. flexion of the hip, knee and ankle joints on a metronome beat) up to 3.7 Hz without phase wandering. There are no previous reports on the outcomes of such participants attempting to perform

this type of AMC above 3.7 Hz. Here, we investigated this AMC task in the range of 3.8 to 5 Hz. Phase wandering can be expected to occur at this frequency range in novices, as their upper rate limit may lie in this range. However, the question of interest is from which of the three types of rate limit this phase wandering stems: the biomechanical, perceptual or coordination rate limit. From previous research, the human perceptual rate limit is reported to be 8–10 Hz (Repp, 2006), as noted above. Thus, phase wandering within the range of 3.8 to 5 Hz cannot be due to the perceptual rate limit. If it is due to the biomechanical rate limit, phase wandering should not occur under the participant's maximal movement frequency. However, if it is due to the coordination rate limit, phase wandering can occur below the maximal movement frequency of the participant. The purpose of this study was to investigate whether the upper rate limit of 1:1 AMC with whole-body oscillation in stance (i.e. the point at which phase wandering occurs) is derived from the biomechanical or coordination rate limit. In addition, we compared skilled street dancers and novices in order to investigate the effect of skill level on the upper rate limit of 1:1 AMC.

MATERIALS AND METHODS

Participants

Seven skilled street dancers (male; age: 26.1±4.6 years) and 10 novice controls (male; age: 25.6±2.1 years) participated in the study. For this experiment, the effect size could not be estimated because no previous studies were available on this measure. We performed *post hoc* power analysis for the interaction using a two-way ANOVA for the frequencies at which AMC rate limit and the maximum frequency of movement were found, which was the main concern in this study (see below), and found the power was 0.74 for this sample size. Hereafter, we refer to the group of skilled dancers as the dancers, and the novices as non-dancers. The dancers had 9.6±4.9 years of dancing experience. Four of the dancers had won celebrated national street dance competitions, and one had won celebrated international street dance competitions. All the non-dancers were graduate students from the human movement science laboratory at the University of Tokyo. They had no experience of any kind of dance. Four of the non-dancers had participated in national championships in sports, and five had participated in local championships in sports. After ceasing to be competitive players, they had been enjoying sports at a recreational level. Thus, fitness level may be assumed not to have differed markedly between the groups. Informed consent for their participation was obtained from all participants prior to the experiment. This study was in accordance with the Declaration of Helsinki and approved by the Ethics Committee of the Graduate School of Arts and Sciences at the University of Tokyo.

Apparatus

An electrogoniometer (Biopac Systems, Tokyo, Japan) was attached to the participant's right knee. Larger values in the data output signified knee extension and smaller values signified knee flexion. A metronome beat was provided using a DB-90 Dr Beat metronome (Roland, Shizuoka, Japan). Electrogoniometer and metronome beat signals were sampled at 1000 Hz with an MP100 recording system (Biopac Systems) and recorded on a personal computer using a specialised software package (AcqKnowledge 3.7.3 for Windows; Biopac Systems).

Procedure

Participants were instructed to flex the hip, knee and ankle joints on the metronome beat in stance. This is called 'down-on-the-beat'

coordination (Miura et al., 2013a, 2011). The beat frequency ranged from 3.8 to 5 Hz in steps of 0.17 Hz. Each beat frequency was used for a single trial. The order of trials was randomised. Each trial lasted about 15 s, during which time the participant attempted down-on-the-beat coordination for at least 10 s. Data recorded during these 10 s were analysed. Between trials, the participants were allowed to rest for as long as they needed in order not to feel any fatigue.

Analysis

Rate limit for AMC

First, in order to investigate whether or not the AMC rate limit is due to the biomechanical rate limit, we calculated and compared the AMC rate limit and the maximum frequency of movement (f_{\max}). The AMC rate limit is the maximum beat frequency at which the participants could perform the task successfully. If 90% of the auditory beats in a trial coincided with the knee-flexion phase, the trial was treated as a successful one. In trials where 90% of the auditory beats coincided with the flexion phase, the chi-squared test with one degree of freedom rejected the null hypothesis (i.e. the phase angles were uniformly distributed) at $P < 0.001$ for each beat frequency (e.g. $\chi^2 = 16$, $P < 10^{-4}$, when the beat frequency is 5 Hz). The highest beat frequency among the successful trials was defined as the AMC rate limit for that participant.

f_{\max}

As we could not measure the biomechanical rate limit of this task directly, we used the f_{\max} among all trials for the analysis. This was because some of the dancers had a dance technique called the vibration technique, in which they exhibited tremor by flexing and extending the knees very quickly within a very small angular range, with high muscle co-contraction. This technique is usually performed with the beat of sound effect around 10 Hz that is incorporated into music although it has not been investigated whether the frequency of the vibration technique matches the beat frequency. This technique is qualitatively different from the movement of novices. Thus, we calculated the f_{\max} for the analysis, and compared it with the AMC rate limit. If the AMC rate limit did not differ from the f_{\max} , phase wandering could be attributed to the biomechanical rate limit. If the AMC rate limit was smaller than the f_{\max} , the constraint causing phase wandering must lie in the auditory-motor system. Movement frequency was calculated using an autocorrelation function (ACF) of knee angular displacement (Nelson-Wong et al., 2009) that was smoothed by a forward and backward second-order Butterworth low-pass filter with a cut-off frequency of 10 Hz. The time shift of the first peak value of the ACF gives movement frequency.

Frequency difference relative to beat frequency

In order to examine whether a coordination rate limit exists, we also calculated the frequency difference (Δf) between movement frequency and either f_{\max} or beat frequency, whichever was the smaller value (Fig. 1). When the movement frequency was smaller than the beat frequency or the f_{\max} , the polarity of Δf had a negative value. A Δf less than 0 indicated that movement frequency was reduced in comparison to beat frequency, even though the participant could oscillate at a higher frequency. In this case, there exists a coordination rate limit per se. A Δf of 0 indicated that when movement was delayed relative to the beat frequency, this was only as a result of the f_{\max} . According to this calculation method, the Δf was defined at seven beat frequencies other than the beat frequency at which the f_{\max} was observed in most of the participants. This is because the f_{\max} of these participants was below the beat frequency

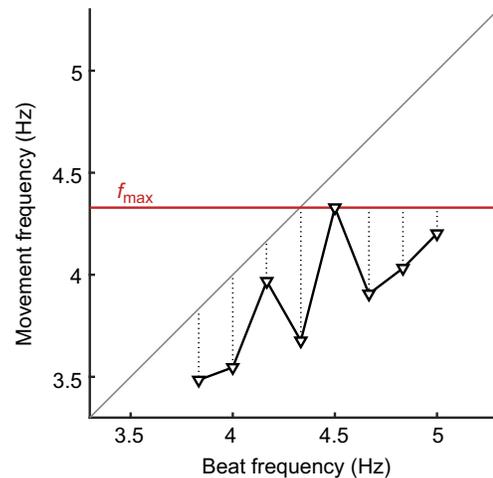


Fig. 1. Calculation method for the frequency difference, Δf . Movement frequency is shown as a function of beat frequency for a non-dancer with the greatest frequency reduction (i.e. the smallest Δf) among all the participants. Δf is the frequency difference between the movement frequency and the smaller value of the maximum movement frequency (f_{\max}) and the beat frequency. The dotted line indicates Δf . When the movement frequency is smaller than the beat frequency or the f_{\max} , the polarity of Δf has a negative value. A Δf less than 0 indicates that movement frequency is reduced in comparison to beat frequency, even though the participant could oscillate at a higher frequency. A Δf of 0 indicates that when the movement frequency is reduced relative to the beat frequency, this is only as a result of the f_{\max} .

at which the f_{\max} was observed, as showed in Fig. 1. In such a case, the Δf could not be defined at the beat frequency where the f_{\max} was observed. The f_{\max} varied among the participants, which means that the defined value of Δf varied. Thus, we defined Δf at seven beat frequencies other than the beat frequency where the f_{\max} was observed in all the participants, and averaged the values across the seven beat frequencies within a participant.

Auditory-motor performance

In order to quantify the coordination between movement and the beat, we calculated the phase angle of beat onset time in the same way as in previous work (Miura et al., 2016, 2013a, 2011). First, the angular velocity of the knee was obtained by differentiating angular displacement. Movement trajectory was reconstructed on a phase plane composed of angular displacement and velocity that were converted to Z-values for a specific duration (beat onset time \pm half beat period). Then, the phase angle at each beat onset, defined as $\phi = \arctan(\omega/\theta)$, was calculated, where ω is the angular velocity and θ is the angular displacement. The standard deviation of the phase angle (s.d. of ϕ) was calculated using circular statistics (Batschelet, 1981).

In order to quantify the extent of phase wandering, we calculated the range of the unwrapped phase angle (range of ϕ); that is, the difference between the maximum and minimum phase angle during a trial. The polarity of the range of ϕ was determined by linear least-squares approximation of the time series of the unwrapped phase angle. A negative range of ϕ indicated that the participant had oscillated at a frequency that was higher than the beat frequency, and a positive range of ϕ meant that the participant had oscillated at a frequency that was lower than the beat frequency.

Kinematics

Because knee angular displacement jittered at high movement frequencies in some participants, it was technically difficult to define its amplitude. In addition, using the Kolmogorov-Smirnov

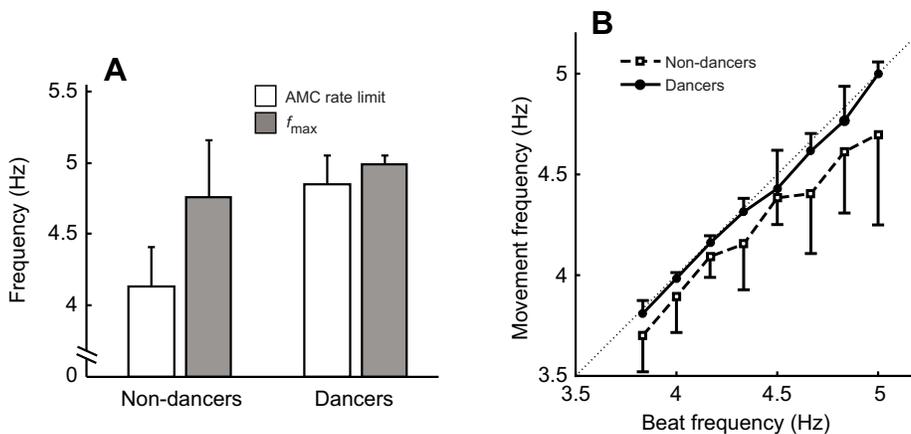


Fig. 2. Auditory–motor coordination rate limit and movement frequency Group means \pm s.d. are shown ($N=10$ for non-dancers, $N=7$ for dancers). (A) Auditory-motor coordination (AMC) rate limit and maximum movement frequency (f_{max}) by group. Only the non-dancers showed a significant difference between AMC rate limit and f_{max} (Bonferroni corrected $P=0.001$). (B) Movement frequency as calculated by autocorrelation function. We found an almost significant main effect of group using a two-way ANOVA performed on movement frequency ($P=0.08$). This implies that the movement frequency tended to differ between the groups.

test, we confirmed that knee angular displacement was not normally distributed. Thus, the extent of knee flexion during the task was quantified by the median knee angular displacement, and the amplitude of knee angular displacement was estimated by the interquartile range (IQR) of knee angular displacement.

Statistics

In order to compare the frequencies at which the AMC rate limit and the f_{max} were found in each group, a two-way ANOVA with one between-subjects factor (group: dancer versus non-dancer) and one within-subjects factor (AMC rate limit versus f_{max}) was conducted. A two-way ANOVA with one between-subjects factor (group: dancer versus non-dancer) and one within-subjects factor (beat frequency: 3.8 to 5 Hz in steps of 0.17 Hz) was conducted on the s.d. of ϕ , range of ϕ , movement frequency and kinematic variables. For this ANOVA, when Mauchly's test of sphericity showed heterogeneity of covariance, the more conservative Greenhouse–Geisser test was employed. An unpaired Welch's test was conducted on Δf to compare the dancers and the non-dancers. The Δf of each group was also compared to 0 using a two-tailed one-sample t -test. The level of statistical significance was set at $P<0.05$.

RESULTS

AMC rate limit versus f_{max}

Fig. 2A shows the AMC rate limit and the f_{max} for each group. Because a two-way ANOVA revealed a significant interaction ($F_{1,15}=8.769$, $P=0.010$; partial η^2 , $\eta_p^2=0.369$), we performed two-tailed paired t -tests to compare the AMC rate limit and the f_{max} within each group. There was a significant difference between the AMC rate limit and the f_{max} in the non-dancers (Bonferroni-corrected $P=0.001$) but not in the dancers (Bonferroni-corrected $P=0.336$). This indicates that phase wandering, or the point at which the AMC rate limit is reached, is not due to the biomechanical rate limit in the non-dancers. In other words, there exists a coordination rate limit. An unpaired Welch's test was conducted on these variables for comparison of the groups. There was a significant difference between the groups in their AMC rate limit (Bonferroni-corrected $P<0.001$) but not in their f_{max} (Bonferroni-corrected $P=0.195$). This suggests that the AMC rate limit had increased through long-term training in street dance in the dancers.

Movement frequency and Δf

Fig. 2B shows movement frequency (i.e. the time shift of the first peak value of the ACF) as a function of beat frequency (see Fig. S1 for the first peak value of the ACF). A two-way ANOVA revealed

no significant interaction ($F_{2,688,40,324}=1.216$, $P=0.314$, $\eta_p^2=0.075$). A main effect of group was almost significant ($F_{1,15}=3.525$, $P=0.08$, $\eta_p^2=0.190$). There was significant main effect of beat frequency ($F_{2,688,40,324}=97.563$, $P<0.001$, $\eta_p^2=0.867$).

The Δf was -0.12 ± 0.12 Hz (mean \pm s.d.) in the non-dancers and -0.04 ± 0.07 Hz in the dancers. An unpaired Welch's test was conducted on Δf for comparison of the groups. There was no significant difference between the groups in the Δf ($P=0.104$). One-sample t -tests revealed a significant difference between Δf and 0 in the non-dancers ($P=0.013$) but not in the dancers ($P=0.237$). This means that the non-dancers lagged behind the beat, even though they could physically oscillate at a higher frequency. This also indicates that the AMC rate limit was not due to the biomechanical rate limit in the non-dancers.

Phase angle of beat time

Fig. 3 shows a histogram of ϕ of all participants as a function of beat frequency. Phase wandering was typically observed in the non-dancers (Fig. 3A). Fig. 4A shows the s.d. of ϕ as a function of beat frequency. A two-way ANOVA revealed no significant interaction ($F_{7,105}=1.828$, $P=0.089$, $\eta_p^2=0.109$). The main effect of group was significant ($F_{1,15}=16.746$, $P=0.001$, $\eta_p^2=0.527$). This means that the dancers performed the task more stably than the non-dancers. The main effect of beat frequency was significant ($F_{7,105}=7.009$, $P<0.001$, $\eta_p^2=0.318$).

Fig. 4B shows the range of ϕ as a function of beat frequency. A two-way ANOVA revealed that there was no significant interaction ($F_{2,475,37,127}=0.504$, $P=0.647$, $\eta_p^2=0.032$), main effect

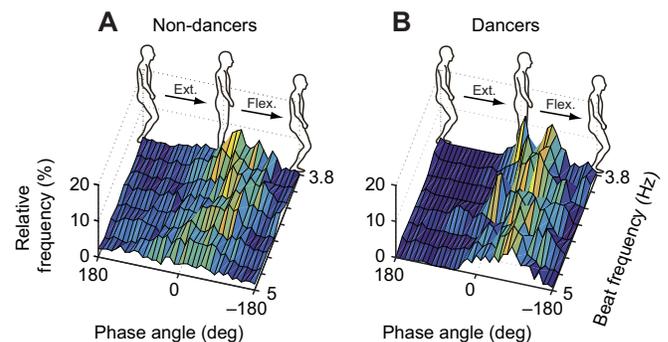


Fig. 3. Relative frequency of the phase angle of beat time in non-dancers and dancers. The non-dancers ($N=10$; A) showed a greater extent of phase wandering for a wide range of beat frequencies, whereas the dancers ($N=7$; B) did not. Ext., extension; Flex., flexion.

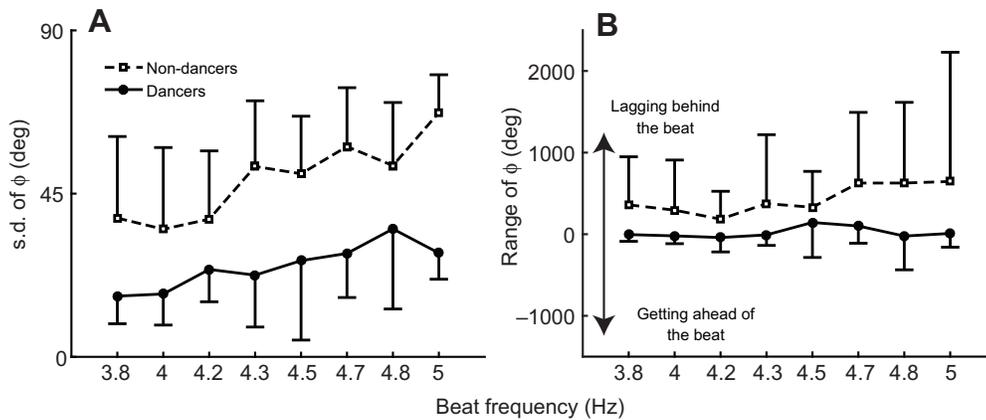


Fig. 4. Phase angle (ϕ) of beat time. Group means \pm s.d. ($N=10$ for non-dancers, $N=7$ for dancers). A two-way ANOVA performed on the s.d. of ϕ (A) revealed a significant main effect of group ($P=0.001$). The range of ϕ (B) did not differ between the groups ($P=0.116$).

of group ($F_{1,15}=2.779$, $P=0.116$, $\eta_p^2=0.156$) or main effect of beat frequency ($F_{2,475,37,127}=0.656$, $P=0.556$, $\eta_p^2=0.042$).

Kinematics

Fig. 5A shows the extent of knee flexion as a function of beat frequency. A two-way ANOVA revealed no significant interaction ($F_{7,105}=1.021$, $P=0.421$, $\eta_p^2=0.064$). A main effect of group was almost significant ($F_{1,15}=4.099$, $P=0.061$, $\eta_p^2=0.215$). There was significant main effect of beat frequency ($F_{7,105}=8.062$, $P<0.001$, $\eta_p^2=0.350$).

Fig. 5B shows the IQR of knee angular displacement (i.e. an estimation of the amplitude of knee angular displacement) as a function of beat frequency. A two-way ANOVA revealed no significant interaction ($F_{7,105}=0.373$, $P=0.916$, $\eta_p^2=0.024$). No significant main effect of group was found ($F_{1,15}=0.009$, $P=0.925$, $\eta_p^2=0.001$). There was significant main effect of beat frequency ($F_{7,105}=28.616$, $P<0.001$, $\eta_p^2=0.656$). This means that the amplitude of knee angular displacement did not differ between groups.

Mediation analysis

Interestingly, we found almost significant differences in the extent of knee flexion between the groups ($P=0.061$). The non-dancers flexed their knees more during oscillation than did the dancers and, at the same time, the amplitude of knee angular displacement did not differ between the groups. Thus, there arises a question about

whether the extent of knee flexion is related to AMC performance. There is a possibility that, for some reason, the non-dancers could not adjust the extent of their knee flexion properly during the task, and that in the case where they flexed their knees more, more torque on the joint was needed in order to oscillate with a certain movement amplitude and frequency. Because there is an upper limit for joint torque, this may have led to a lower maximum movement frequency and a certain frequency reduction relative to the beat (i.e. the smaller f_{max} and Δf), which in turn led to poorer performance (i.e. the greater s.d. and range of ϕ , and the lower AMC rate limit). To test this hypothesis, we conducted a mediation analysis by treating the variables of all participants as a continuous variable. In this experiment, it seems that the task difficulty was insufficient to pinpoint the skill level of the task, for the following two reasons. First, the AMC rate limit was 5 Hz in four of the dancers (the average for the dancers was 4.9 Hz). Second, the extent of phase wandering (i.e. range of ϕ) did not differ significantly between the groups (Fig. 4B), although the non-dancers showed significantly greater phase angle variability (i.e. s.d. of ϕ ; Fig. 4A). If the task had been more difficult (that is, if the beat frequency had been higher), we would have found a significant difference between the groups on more measures (e.g. the f_{max} , movement frequency, range of ϕ and extent of knee flexion). Thus, we combined the two groups for the mediation analysis.

We performed mediation analysis using ordinary least-squares path analysis (Hayes, 2013). As diagrammed in Fig. 6, we

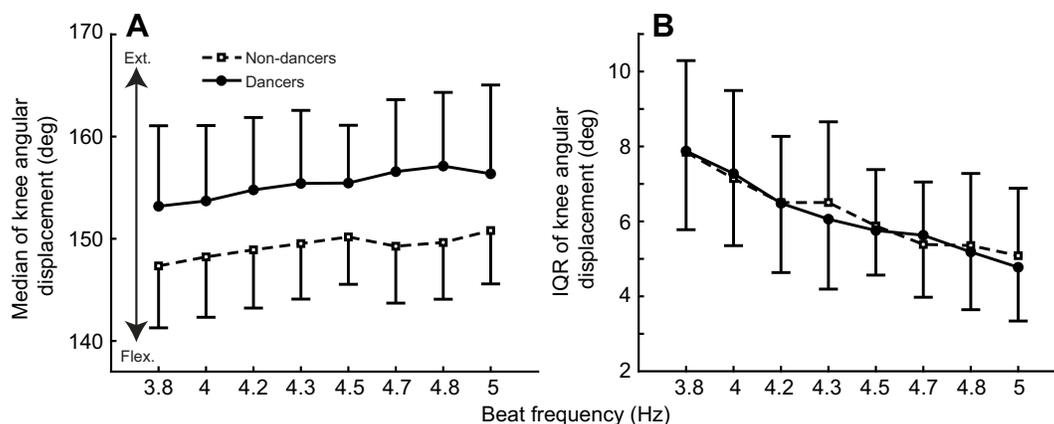


Fig. 5. Kinematic variables. Group mean \pm s.d. ($N=10$ for non-dancers, $N=7$ for dancers). A two-way ANOVA performed on the median knee angular displacement (A) revealed an almost significant main effect of group ($P=0.061$). This implies that the non-dancers tended to flex their knees more during the task. The IQR (B) did not differ between the groups ($P=0.925$).

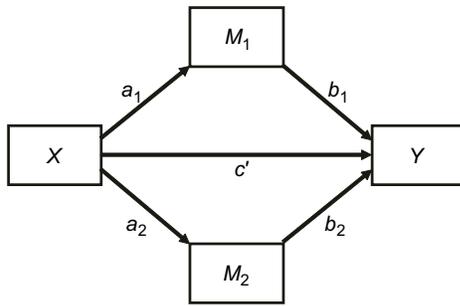


Fig. 6. Diagram of mediation analysis. Three separate mediation analyses were conducted for three performance measures (Y : s.d. of ϕ , range of ϕ or AMC rate limit). In all mediation analysis, X is the extent of knee flexion, M_1 is Δf and M_2 is f_{\max} .

hypothesized that greater knee flexion (X) leads to poorer performance (Y ; i.e. greater s.d. of ϕ and range of ϕ , or lower AMC rate limit) through its effect on Δf (M_1) and f_{\max} (M_2). We conducted three separate mediation analyses, one for each performance variable. We included all measured variables as covariates in the model of both M and Y . We averaged the extent of knee flexion, the IQR of knee angular displacement, the s.d. of ϕ and the range of ϕ across all beat frequencies for mediation analysis, because a two-way ANOVA revealed no significant interaction between group and beat frequency. Because we did not find a significant correlation between M_1 and M_2 after adjusting X ($P=0.087$), we used a parallel multiple mediator model. The results are summarized in Table S1.

The results for s.d. of ϕ were as follows. Participants who flexed their knees more exhibited a greater frequency reduction (a smaller Δf ; $a_1=0.010$), and participants whose frequency reduction was larger exhibited poorer performance (i.e. a greater s.d. of ϕ ; $b_1=-103.752$). A bias-corrected bootstrap confidence interval that was calculated for the indirect effect ($a_1b_1=-0.983$) using 10,000 bootstrap samples lay entirely below zero (-2.170 to -0.294), which provides evidence of an indirect effect of the extent of knee flexion on performance through Δf (M_1). The direct effect of the extent of knee flexion on this performance measure was not significant ($c'=-0.210$, $P=0.692$). This means that the extent of knee flexion did not affect performance (i.e. the s.d. of ϕ) independently of the mediator (M_1).

The results for range of ϕ were as follows. Participants who flexed their knees more showed a greater frequency reduction (a smaller Δf ; $a_1=0.010$) and lower f_{\max} ($a_2=0.023$), and participants whose frequency reduction was larger exhibited poorer performance (i.e. a larger range of ϕ ; $b_1=-3073.791$). Additionally, participants whose f_{\max} was lower exhibited poorer performance (i.e. larger range of ϕ ; $b_2=-786.442$). Bias-corrected bootstrap confidence intervals calculated for the indirect effects ($a_1b_1=-29.120$ and $a_2b_2=-18.294$, respectively) using 10,000 bootstrap samples lay entirely above zero (-60.950 to -10.411 and -46.212 to -2.261 , respectively), which provides evidence of indirect effects of the extent of knee flexion on performance through Δf (M_1) and f_{\max} (M_2). The direct effect of the extent of knee flexion on this performance measure was not significant ($c'=7.733$, $P=0.419$). This means that the extent of knee flexion did not affect performance (i.e. the range of ϕ) independently of the mediators (M_1 and M_2).

There were no significant indirect effects of the extent of knee flexion on AMC rate limit through Δf (M_1) or f_{\max} (M_2). Bias-corrected bootstrap confidence intervals that were calculated

for the indirect effects ($a_1b_1=0.016$ and $a_2b_2=0.002$, respectively) using 10,000 bootstrap samples included zero (-0.022 to 0.048 and -0.015 to 0.030 , respectively). The direct effect of the extent of knee flexion on this performance measure was not significant ($c'=0.024$, $P=0.159$). These findings mean that the extent of knee flexion did not affect performance (i.e. AMC rate limit), either directly or indirectly.

In order to examine the direction of causal flow in these mediation models, we conducted an alternative mediation analysis by exchanging X and Y . We found no evidence of indirect effects or of direct effects for the three performance measures. These results indicate the existence of a directed causal flow from X to Y through the mediators.

DISCUSSION

We investigated whether the upper rate limit of 1:1 AMC is due to either the biomechanical rate limit or the coordination rate limit, and the effect of skill level on this limit, by comparing skilled street dancers and novices. Our findings suggest that the AMC rate limit cannot be attributed to the biomechanical rate limit; that is, there exists a coordination rate limit per se in the whole-body AMC task. The dancers exhibited a significantly higher AMC rate limit than that of the non-dancers. Additionally, only in the non-dancers was the AMC rate limit significantly lower than the maximum movement frequency. These results suggest that the dancers enhanced their coordination rate limit to the level of their maximum movement frequency. In addition, in the mediation analysis, we found that the extent of knee flexion operates as a constraint for this type of whole-body AMC performed under gravity, which can be overcome by long-term practice. Below, we discuss these findings in turn, and offer suggestions for cross-species research.

Coordination rate limit

In previous research (Repp, 2006), the upper AMC rate limit has tended to be regarded as resulting from a bottleneck of the biomechanical and perceptual rate limits. Because the biomechanical rate limit is lower than the perceptual rate limit, the former has been regarded as the AMC rate limit. However, here we provide evidence that the rate limit of 1:1 AMC cannot be attributed to the biomechanical rate limit in the non-dancers. We confirmed that the AMC rate limit was significantly lower than the maximum movement frequency in the non-dancers (Fig. 2A). Moreover, we observed Δf significantly below 0 in the non-dancers. This means that the movement frequency fell behind the beat frequency, at a lower frequency than their maximum. These findings suggest that the upper rate limit for 1:1 AMC is due to a coordination rate limit per se – i.e. it does not result from a bottleneck of the biomechanical and perceptual rate limits – in the non-dancers. In other words, there is a beat frequency at which humans can perceive the beat precisely, and have the capability to oscillate at a higher frequency than prescribed, but cannot coordinate the oscillatory movement to the beat as they intend during rapid AMC.

Effect of skill level

A similar phenomenon to our findings occurs at lower frequencies (Miura et al., 2016, 2013a, 2011). When participants were instructed to perform an AMC task called ‘up-on-the-beat’ coordination, in which the hip, knee and ankle joints are extended on the beat in stance, their coordination pattern was unintentionally entrained to a down-on-the-beat pattern at frequencies above 2 Hz (Miura et al., 2013a). That is, they could perceive the beat precisely, and could oscillate at the same frequency as the beat, but they could

not coordinate the oscillatory movement with the beat as intended. This is a common characteristic of human AMC above a certain frequency, and is attributed to a constraint that underlies the AMC process.

Miura et al. (2011) investigated the effect of skill level on up-on-the-beat coordination, and showed that skilled street dancers could achieve the intended AMC by overcoming such constraints. Here, we found that the AMC rate limit was lower than the maximum movement frequency only in the non-dancers (Fig. 2A). This suggests that the dancers may have overcome a constraint on the AMC process and could coordinate their oscillatory movement to the beat as they intended at higher frequencies. This AMC learning process, in which novices who have the capacity to oscillate at a high enough frequency to match their movement to the beat are able, with practice, to overcome a constraint on the AMC process and obtain the ability to coordinate their movement to the beat in the manner they intend, is expected to be common (Miura et al., 2016, 2013a, 2011). This should be confirmed in a longitudinal study. A noteworthy result from the present study was that the world champion participant did not lose AMC at any beat frequency in the experiment and performed the task perfectly; that is, all the beats in all his trials coincided with the knee flexion phase. In a future study, we intend to investigate how he is able to retain AMC at higher frequencies after long-term practice of street dancing. One possibility is that, when the constraint on the AMC process itself is overcome, the biomechanical rate limit and AMC rate limit no longer differ.

Kinematic bias

Although this outcome was unexpected, we identified a component of one constraint on the AMC process, namely a kinematic bias. Interestingly, we identified a causal relationship between kinematics and AMC performance. In the mediation analysis, we found a causal flow by which participants who flexed their knees more exhibited a larger frequency reduction and a lower maximum movement frequency. A larger frequency reduction indicates lagging behind the beat more at a lower frequency than the participant's maximum movement frequency. These effects in turn led to greater phase angle variability and a higher level of phase wandering. This causal flow is reasonable because when the knees are flexed more in stance in the gravitational field, more joint torque is needed to oscillate to achieve a certain movement amplitude and frequency. Considering that the kinematic bias was salient in the non-dancers, it seems reasonable that they would require it for controlling this AMC. For example, they may require augmented proprioceptive feedback from the thigh muscles by flexing their knees more. Thus, kinematic bias can be one of the constraints for coordination rate limit. Our findings provide the first evidence that this kinematic bias in the gravitational field acts as a constraint on AMC.

Gravity as a common constraint for AMC involving vertical movement

We found that the loss of AMC around the upper rate limit could be partly attributed to kinematic bias in the direction of gravity. This suggests that gravity acts as a constraint on rapid AMC. Previous research on human AMC shows that the coordination pattern in which downward movement is matched with the beat (down-on-the-beat coordination) emerges at high movement frequencies even when the participants intend to coordinate in a different pattern (Miura et al., 2016, 2013a, 2011). Carson et al. (2009) demonstrated that this is due to the effect of gravity by manipulating it using a robotic device. Similarly, gravity seems to act as a constraint on

AMC in sea lions. In Cook et al.'s (2013) study, the sea lion subject showed tempo flexibility, and could synchronise vertical bobbing movement to the beat at different frequencies. The noteworthy result is that a down-on-the-beat pattern emerged at the fastest tempo that they tested (132 bpm). Taking this together with the present findings, we suggest that gravity can act as common constraint on rapid AMC involving rhythmic vertical movement in humans and other species.

Effect of natural frequency difference on AMC

As mentioned in the Introduction, cross-species comparison of AMC with morphologically similar movements would lead to greater understanding of the evolution of AMC. Thus, it is important to observe whole-body AMC in humans directly and to find commonalities and/or differences between AMC involving the finger and the whole body in humans. For the non-dancers, the rate limit of 1:1 AMC for this task was 4.1 Hz, which is lower than that of finger oscillation. This is reasonable, considering the lower natural frequency of whole-body movement relative to that of finger movement. In addition, this is consistent with previous research (Miura et al., 2016, 2013a). In AMC achieved by novices, the phase transition from up-on-the-beat to down-on-the-beat occurs at 2.6 Hz in finger oscillation (Miura et al., 2016) and at 2.1 Hz in whole-body oscillation under conditions of ascending beat frequency (Miura et al., 2013a). This may be because when the difference between beat frequency and the natural frequency of the effector is greater, the phase between movement oscillation and the beat becomes 'de-tuned' more easily, which leads to phase transition or loss of AMC (i.e. phase wandering). These findings suggest that the natural frequency of movement of the body parts involved in coordination with the beat can be a constraint on the stability of AMC. We suggest that for cross-species comparison of AMC, the varying natural frequencies of body movement in different animals should also be taken into consideration. Loss of AMC can be merely due to the natural frequency of the body differing from the beat frequency.

Conclusion

We confirmed that the 1:1 AMC upper rate limit is due to the coordination rate limit; that is, it does not just result from a bottleneck of biomechanical and perceptual rate limits but rather there exists a constraint within the AMC process itself. We provide evidence that one of the constraints on the coordination rate limit may be a kinematic bias – the extent of knee flexion during oscillation – in the gravitational field. In addition, we found that the tempo flexibility was extended in the dancers versus the non-dancers. The dancers may have overcome a constraint such as kinematic bias in the AMC process and increased their AMC rate limit. Such a learning process, in which a constraint that is imposed on coordination is overcome, is a common characteristic of sensorimotor learning in various kinds of rhythmic coordination (Fujii et al., 2010; Miura et al., 2015; Swinnen, 2002). This study offers suggestions for the investigation of what causes the loss of AMC in non-human animals. We believe that direct observation of AMC involving whole-body oscillation is needed in order to facilitate cross-species comparison, because this would enable us to compare AMC involving morphologically similar body parts among various kinds of animals.

Acknowledgements

We acknowledge the helpful comments of Dr Keita Kamijo at Waseda University and Dr Hiroyuki Sasai at the University of Tokyo for statistical analysis.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: A.M., K.K., K.N.; Methodology: A.M., S.F., M.O., K.K., K.N.; Software: A.M., S.F., M.O.; Validation: A.M., M.O.; Formal analysis: A.M., S.F., M.O.; Writing - original draft: A.M., S.F.; Writing - review & editing: A.M., S.F., M.O., K.K., K.N.; Supervision: K.K., K.N.; Project administration: A.M., K.K., K.N.; Funding acquisition: A.M.

Funding

This research was partly supported by Grants-in-Aid from the Japan Society for the Promotion of Science (JSPS) for JSPS Fellows awarded to A.M. (no. 23-9480 and no. 25-6687), and by financial aid from Advanced Research Center for Human Sciences, Waseda University to A.M. as a member of the Research Project C, 'A basic and applied study of movements based on Bernstein's idea of coordination' (PI: Nobuhiro Furuyama).

Data availability

Data are available from the Dryad Digital Repository (Miura et al., 2018): <https://doi.org/10.5061/dryad.4dh955q>

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.179457.supplemental>

References

- Batschelet, E.** (1981). *Circular Statistics in Biology*. New York: Academic Press Inc.
- Bood, R. J., Nijssen, M., van der Kamp, J. and Roerdink, M.** (2013). The power of auditory-motor synchronization in sports: enhancing running performance by coupling cadence with the right beats. *PLoS ONE* **8**, e70758.
- Bregman, M. R., Iversen, J. R., Lichman, D., Reinhart, M. and Patel, A. D.** (2013). A method for testing synchronization to a musical beat in domestic horses (*Equus ferus caballus*). *Empir. Musicol. Rev.* **7**, 144-156.
- Byblow, W. D., Carson, R. G. and Goodman, D.** (1994). Expressions of asymmetries and anchoring in bimanual coordination. *Hum. Movement Sci.* **13**, 3-28.
- Carroll, T. J., Benjamin, B., Stephan, R. and Carson, R. G.** (2001). Resistance training enhances the stability of sensorimotor coordination. *Proc. R. Soc. Lond. B* **268**, 221-227.
- Carson, R. G., Oytam, Y. and Riek, S.** (2009). Artificial gravity reveals that economy of action determines the stability of sensorimotor coordination. *PLoS ONE* **4**, e5248.
- Cook, P., Rouse, A., Wilson, M. and Reichmuth, C.** (2013). A California sea lion (*Zalophus californianus*) can keep the beat: motor entrainment to rhythmic auditory stimuli in a non vocal mimic. *J. Comp. Psychol.* **127**, 412-427.
- Fink, P. W., Foo, P., Jirsa, V. K. and Kelso, J. A. S.** (2000). Local and global stabilization of coordination by sensory information. *Exp. Brain Res.* **134**, 9-20.
- Fujii, S., Kudo, K., Ohtsuki, T. and Oda, S.** (2010). Intrinsic constraint of asymmetry acting as a control parameter on rapid, rhythmic bimanual coordination: a study of professional drummers and non-drummers. *J. Neurophysiol.* **104**, 2178-2186.
- Fujii, S., Watanabe, H., Oohashi, H., Hirashima, M., Nozaki, D. and Taga, G.** (2014). Precursors of dancing and singing to music in three- to four-months-old infants. *PLoS ONE* **9**, e97680.
- Hasegawa, A., Okanoya, K., Hasegawa, T. and Seki, Y.** (2011). Rhythmic synchronization tapping to an audio-visual metronome in budgerigars. *Sci. Rep.* **1**, 120.
- Hattori, Y., Tomonaga, M. and Matsuzawa, T.** (2013). Spontaneous synchronized tapping to an auditory rhythm in a chimpanzee. *Sci. Rep.* **3**, 1566.
- Hayes, A. F.** (2013). *Introduction to Mediation, Moderation, and Conditional Process Analysis: A Regression-Based Approach*. New York: Guilford Press.
- Hoeschele, M., Merchant, H., Kikuchi, Y., Hattori, Y. and ten Cate, C.** (2015). Searching for the origins of musicality across species. *Philos. Trans. R. Soc. B* **370**, 20140094.
- Honing, H., ten Cate, C., Peretz, I. and Trehub, S. E.** (2015). Without it no music: cognition, biology and evolution of musicality. *Philos. Trans. R. Soc. B* **370**, 20140088.
- Kelso, J. A. S., DelColle, J. D. and Schönner, G.** (1990). Action-perception as a pattern formation process. In *Attention and performance XIII: Motor representation and control*, Vol. 5 (ed. M. Jeannerod), pp. 139-169. Hillsdale, NJ: Lawrence Erlbaum Associates.
- Kudo, K., Park, H., Kay, B. A. and Turvey, M. T.** (2006). Environmental coupling modulates the attractors of rhythmic coordination. *J. Exp. Psychol. Hum. Percept. Perform.* **32**, 599-609.
- McNeill, W. H.** (1997). *Keeping Together in Time*. Cambridge: Harvard University Press.
- Miura, A., Kudo, K., Ohtsuki, T. and Kanehisa, H.** (2011). Coordination modes in sensorimotor synchronization of whole-body movement: a study of street dancers and non-dancers. *Hum. Movement Sci.* **30**, 1260-1271.
- Miura, A., Kudo, K. and Nakazawa, K.** (2013a). Action-perception coordination dynamics of whole-body rhythmic movement in stance: a comparison study of street dancers and non-dancers. *Neurosci. Lett.* **544**, 157-162.
- Miura, A., Kudo, K., Ohtsuki, T., Kanehisa, H. and Nakazawa, K.** (2013b). Relationship between muscle cocontraction and proficiency in whole-body sensorimotor synchronization: a comparison study of street dancers and non-dancers. *Motor Control* **17**, 18-33.
- Miura, A., Kudo, K., Ohtsuki, T. and Nakazawa, K.** (2014). Effects of long-term practice on coordination between different joint motions in street dancers. *Arts BioMech.* **2**, 55-65.
- Miura, A., Fujii, S., Yamamoto, Y. and Kudo, K.** (2015). Motor control of rhythmic dance from a dynamical systems perspective: a review. *J. Dance Med. Sci.* **19**, 11-21.
- Miura, A., Fujii, S., Okano, M., Kudo, K. and Nakazawa, K.** (2016). Finger-to-beat coordination skill of non-dancers, street dancers, and the world champion of a street-dance competition. *Front. Psychol.* **7**, 542.
- Miura, A., Fujii, S., Okano, M., Kudo, K. and Nakazawa, K.** (2018). Data from: Upper rate limits for one-to-one auditory-motor coordination involving whole-body oscillation: a study of street dancers and non-dancers. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.4dh955q>.
- Nakata, H., Yoshie, M., Miura, A. and Kudo, K.** (2010). Characteristics of the athletes' brain: evidence from neurophysiology and neuroimaging. *Brain Res. Rev.* **62**, 197-211.
- Nelson-Wong, E., Howarth, S., Winter, D. A. and Callaghan, J. P.** (2009). Application of autocorrelation and cross-correlation analyses in human movement and rehabilitation research. *J. Orthop. Sports Phys. Ther.* **39**, 287-295.
- Patel, A. D.** (2014). The evolutionary biology of musical rhythm: was Darwin wrong? *PLoS Biol.* **12**, e1001821.
- Patel, A. D., Iversen, J. R., Bregman, M. R. and Schulz, I.** (2009). Experimental evidence for synchronization to a musical beat in a nonhuman animal. *Curr. Biol.* **19**, 827-830.
- Repp, B. H.** (2005). Sensorimotor synchronization: a review of the tapping literature. *Psychon. Bull. Rev.* **12**, 969-992.
- Repp, B. H.** (2006). Rate limits of sensorimotor synchronization. *Adv. Cogn. Psychol.* **2**, 163-181.
- Schachner, A., Brady, T. F., Pepperberg, I. M. and Hauser, M. D.** (2009). Spontaneous motor entrainment to music in multiple vocal mimicking species. *Curr. Biol.* **19**, 831-836.
- Stout, D. and Chaminade, T.** (2012). Stone tools, language and the brain in human evolution. *Phil. Trans. R. Soc. B* **367**, 75-87.
- Swinnen, S. P.** (2002). Intermanual coordination: from behavioural principles to neural-network interactions. *Nature Rev. Neurosci.* **3**, 348-359.
- Wilson, M. and Cook, P. F.** (2016). Rhythmic entrainment: why humans want to, fireflies can't help it, pet birds try, and sea lions have to be bribed. *Psychon. Bull. Rev.* **23**, 1647-1659.
- Zentner, M. and Eerola, T.** (2010). Rhythmic engagement with music in infancy. *Proc. Natl. Acad. Sci. USA* **107**, 5768-5773.

Supplementary materials

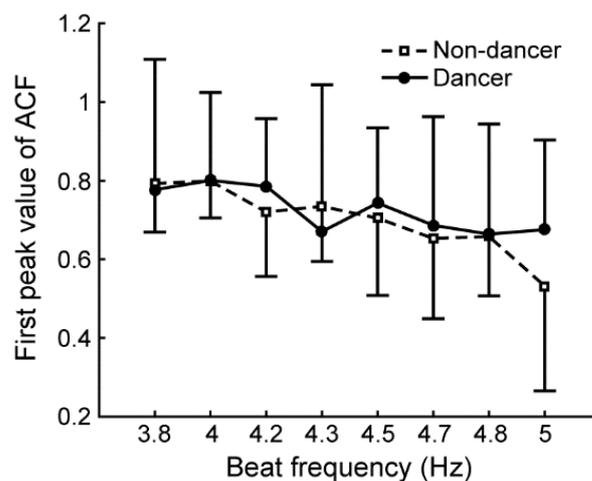


Fig. S1. The first peak value of the autocorrelation function (ACF). Group mean \pm s.d. ($N=10$ for Non-dancers, $N=7$ for Dancers). In order to confirm the validity of the method for detecting movement frequency (i.e., time shift of the first peak value of the ACF), we calculated the first peak value of the ACF. A two-way ANOVA conducted on the first peak value of the ACF revealed no significant interaction between group and beat frequency, $F(3.263, 48.943) = 1.403$, $p = .252$, $\eta_p^2 = .086$. No significant main effect of group was found, $F(1, 15) = .075$, $p = .787$, $\eta_p^2 = .005$. This indicates that the spatio-temporal regularity of knee angular displacement did not differ between the groups, which supports the validity of the method for detecting movement frequency. There was a significant main effect of beat frequency, $F(3.263, 48.943) = 6.590$, $p = .001$, $\eta_p^2 = .305$.

Antecedent	Consequent																			
	$M_1 (\Delta freq)$			$M_2 (f_{max})$			Y (S.d. of φ)			Y (Range of φ)			Y (AMC rate limit)							
	Coeff.	SE	p	Coeff.	SE	p	Coeff.	SE	p	Coeff.	SE	p	Coeff.	SE	p					
X (The extent of knee flexion)	a_1	0.010	0.003	0.014	a_2	0.023	0.011	0.053	c'	-0.210	0.518	0.692	c'	7.733	9.256	0.419	c'	0.024	0.016	0.159
$M_1 (\Delta freq)$	—	—	—	—	—	—	—	—	b_1	-103.752	34.869	0.011	b_1	-3073.791	622.823	<0.001	b_1	1.667	1.080	0.147
$M_2 (f_{max})$	—	—	—	—	—	—	—	—	b_2	-7.117	10.720	0.518	b_2	-786.442	191.471	0.001	b_2	0.071	0.332	0.833
Constant	i_{M1}	-1.521	0.517	0.010	i_{M2}	1.329	1.680	0.442	i_Y	96.879	87.194	0.287	i_Y	2651.262	1557.441	0.113	i_Y	0.589	2.700	0.831
	$R^2 = 0.341$			$R^2 = 0.228$			$R^2 = 0.654$			$R^2 = 0.887$			$R^2 = 0.517$							
	$F(1, 15) = 7.759, p = 0.014$			$F(1, 15) = 4.421, p = 0.053$			$F(3, 13) = 8.188, p = 0.003$			$F(3, 13) = 34.145, p < 0.001$			$F(3, 13) = 4.633, p = 0.021$							

Table S1. Regression coefficients, standard errors, and model summary information for the mediation analyses. We conducted three separate mediation analyses, one for each performance variable (Y). Mediation analysis for the s.d. of φ and the range of φ , revealed a non-significant direct effect, and a significant indirect effect of the extent of knee flexion (X) on the performance variable (Y) through the mediator(s). Mediation analysis for the AMC rate limit, revealed neither significant direct nor indirect effects of the extent of knee flexion (X) on the performance variable (Y).