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

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KEYWORDS: Maximum frequency, Sensorimotor synchronisation, Vertical rhythmic movement, Gravity, Dance

SUMMARY STATEMENT
Upper rate limits for one-to-one auditory-motor coordination do not occur due to a bottleneck of perceptual and biomechanical rate limits, but due to constraints in the coordination process.
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 ten 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 due 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.
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 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; Miura et al., 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; Miura et al., 2011; Miura et al., 2013b; Miura et al., 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 and is 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; Repp, 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 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; Miura et al., 2011) to that of cockatoos (Patel et al., 2009), to compare finger oscillation of humans (for a review, see Repp, 2005) to that of chimpanzees (Hattori et al., 2013), and to compare locomotion of humans (Bood et al., 2013) to 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; Miura et al., 2011; Miura et al., 2013b). 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 gives 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. The second focus of this study was to investigate the effect of skill level on upper rate limit for AMC by recruiting novices and skilled street dancers. 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 assume 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). First, 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. Second, the perceptual rate limit refers to the rate at which one cannot perceive the timing of a rhythmic auditory sequence correctly. When a person is asked to tap with a metronome every two, three, or four beats, loss of AMC happens above a beat frequency of 8–10 Hz. 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. 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 Hz 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). Thus, phase wandering within the range of 3.8 Hz 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 their maximal movement frequency. 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 experiment. 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 an interaction of the two-way ANOVA (Fig. 2A), which was the main concern in this study, and found the power was 0.74 for this sample size. Hereafter, we refer 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; Miura et al., 2011). The beat frequency ranged from 3.8 Hz to 5 Hz in steps of 0.17 Hz. Each beat frequency was used for a single trial. The order of trials was randomized. 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 was 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. 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-square test with one degree of freedom rejects the null hypothesis (i.e., the phase angles were uniformly distributed) at \( p < .001 \) for each beat frequency (e.g., \( \chi^2(1) = 16, p < 10^{-4} \), when the beat frequency is 5 Hz). The highest beat frequency among those of the successful trials was defined as the AMC rate limit for that participant.

Maximum movement frequency

Instead of measuring the biomechanical rate limit, we used the maximum movement frequency \( (f_{\text{max}}) \) among all trials for the analysis, as we could not measure the biomechanical rate limit of this task directly. 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 in music although it has not been investigated whether the frequency of the vibration technique matches with the beat frequency. This technique is qualitatively different from the movement of novices. Thus, we calculated the \( f_{\text{max}} \) for the analysis, and compared it with the AMC rate limit. If the AMC rate limit did not differ from the \( f_{\text{max}} \), phase wandering could be attributed to the biomechanical rate limit. If the AMC rate limit was smaller than the \( f_{\text{max}} \), 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 2nd 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 ($\Delta \text{freq}$) between movement frequency and the smaller value of the $f_{\text{max}}$ and the beat frequency (Fig. 1). When the movement frequency was smaller than the beat frequency or the $f_{\text{max}}$, the polarity of $\Delta \text{freq}$ had a negative value. A $\Delta \text{freq}$ 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 $\Delta \text{freq}$ of 0 indicated that when movement was delayed relative to the beat frequency, this was only as a result of the $f_{\text{max}}$. According to this calculation method, the $\Delta \text{freq}$ was defined at seven beat frequencies other than the beat frequency at which the $f_{\text{max}}$ was observed in most of the participants. This is because the $f_{\text{max}}$ of these participants was below the beat frequency at which the $f_{\text{max}}$ was observed as showed in Fig. 1. In such a case, the $\Delta \text{freq}$ could not be defined at the beat frequency where the $f_{\text{max}}$ was observed. The $f_{\text{max}}$ varied among the participants, which means that the missing value of $\Delta \text{freq}$ varied. Thus, we defined $\Delta \text{freq}$ at seven beat frequencies other than the beat frequency where the $f_{\text{max}}$ was observed in all the participants, and averaged them 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 used in previous work (Miura et al., 2016; Miura et al., 2013a; Miura et al., 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-value for specific duration (beat onset time ± half of beat period). Then, the phase angle at each beat onset, defined as $\phi = \arctan(\omega/\theta)$, was calculated, where $\omega$ was the angular velocity and $\theta$ was the angular displacement. The standard deviation of the phase angle (s.d. of $\phi$) 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 $\phi$): that is, the difference between the maximum and minimum phase angle during a trial. The polarity of the range of $\phi$ was determined by linear least-squares approximation of the time series of the unwrapped phase angle. A negative range of $\phi$ indicated that the participant had oscillated at a frequency that was higher than the beat frequency, and a positive range of $\phi$ meant that the participant had oscillated at a frequency that was lower than the beat frequency.

**Kinematics**

Because knee angular displacement was jittering at high movement frequencies in some participants, it was technically difficult to define the amplitude of the knee angular displacement. In addition, using the Kolmogorov-Smirnov test, we confirmed that knee angular displacement was not normally distributed. Thus, the extent of knee flexion during the task was quantified by median of knee angular displacement, and the amplitude of knee angular displacement was estimated by the interquartile range (i.q.r.) of knee angular displacement.

**Statistics**

In order to compare the frequencies at which the AMC rate limit and the $f_{\text{max}}$ were found in each group, a two-way analysis of variance (ANOVA) with 1 between-subjects factor (group; Dancer vs. Non-dancer) and 1 within-subjects factor (AMC rate limit vs. $f_{\text{max}}$) was conducted. A two-way ANOVA with 1 between-subjects factor (group; Dancer vs. Non-dancer) and 1 within-subjects factor (beat frequency; 3.8 Hz to 5 Hz in steps of 0.17 Hz) was conducted on the s.d. of $\phi$, range of $\phi$, 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 $\Delta f_{\text{freq}}$ to compare the Dancers and the Non-dancers. The $\Delta f_{\text{freq}}$ of each group was also compared to 0 using a two-tailed one-sample $t$-test. The level of statistical significance was set at $p < .05$. 
RESULTS

AMC rate limit vs. $f_{\text{max}}$

Fig. 2A shows the AMC rate limit and the $f_{\text{max}}$ for each group. Because a two-way ANOVA revealed significant interaction, $F(1, 15) = 8.769, p = .010, \eta_p^2 = .369$, we performed two-tailed paired $t$-tests to compare the AMC rate limit and the $f_{\text{max}}$ within each group. There was a significant difference between the AMC rate limit and the $f_{\text{max}}$ in the Non-dancers (Bonferroni-corrected $p = .001$), but not in the Dancers (Bonferroni-corrected $p = .336$). 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 $p < .001$), but not in their $f_{\text{max}}$ (Bonferroni-corrected $p = .195$). This suggests that the AMC rate limit had increased through long-term training in street dance in the Dancers.

Movement frequency and $\Delta f_{\text{freq}}$

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 the electronic supplementary material for the first peak value of the ACF). A two-way ANOVA revealed no significant interaction, $F(2.688, 40.324) = 1.216, p = .314, \eta_p^2 = .075$. A main effect of group was almost significant, $F(1, 15) = 3.525 p = .08, \eta_p^2 = .190$. There was significant main effect of beat frequency, $F(2.688, 40.324) = 97.563, p < .001, \eta_p^2 = .867$.

The $\Delta f_{\text{freq}}$ was $-0.12 \pm 0.12$ Hz (mean ± s.d.) in the Non-dancers and $-0.04 \pm 0.07$ Hz in the Dancers. An unpaired Welch’s test was conducted on $\Delta f_{\text{freq}}$ for comparison of the groups. There was no significant difference between the groups in the $\Delta f_{\text{freq}}$ ($p = .104$). One-sample $t$-tests revealed a significant difference between the $\Delta f_{\text{freq}}$ and 0 in the Non-dancers ($p = .013$), but not in the Dancers ($p = .237$). 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.
The phase angle of beat time

Fig. 3 shows a histogram of the phase angle 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 $\phi$ as a function of beat frequency. A two-way ANOVA revealed no significant interaction, $F(7, 105) = 1.828, p = .089, \eta^2 = .109$. The main effect of group was significant, $F(1, 15) = 16.746, p = .001, \eta^2 = .527$. This means that the Dancers performed the task more stably than the Non-dancers. The main effect of beat frequency was significant, $F(7, 105) = 7.009, p < .001, \eta^2 = .318$.

Fig. 4B shows the range of $\phi$ as a function of beat frequency. A two-way ANOVA revealed that there was no significant interaction, $F(2.475, 37.127) = .504, p = .647, \eta^2 = .032$, main effect of group, $F(1, 15) = 2.779, p = .116, \eta^2 = .156$, or main effect of beat frequency, $F(2.475, 37.127) = .656, p = .556, \eta^2 = .042$.

Kinematics

Fig. 5A shows the extent of knee flexion as a function of beat frequency. A two-way ANOVA revealed no significant interaction, $F(7, 105) = 1.021, p = .421, \eta^2 = .064$. A main effect of group was almost significant, $F(1, 15) = 4.099, p = .061, \eta^2 = .215$. There was significant main effect of beat frequency, $F(7, 105) = 8.062, p < .001, \eta^2 = .350$.

Fig. 5B shows the i.q.r. 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, $F(7, 105) = .373, p = .916, \eta^2 = .024$. No significant main effect of group was found, $F(1, 15) = .009, p = .925, \eta^2 = .001$. There was significant main effect of beat frequency, $F(7, 105) = 28.616, p < .001, \eta^2 = .656$. 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 ($p = .061$). 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 $f_{\text{max}}$ and $\Delta \text{freq}$), which in turn led to poorer performance (i.e., the greater s.d. and range of $\varphi$, and the lower the 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 this 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 $\varphi$) did not differ significantly between the groups (Fig. 4B), although the Non-dancers showed significantly greater phase angle variability (i.e., s.d. of $\varphi$; Fig. 4A). If the task had been more difficult (that is, if the beat frequency had been higher), we would have found significant difference between the groups on more measures (e.g., the $f_{\text{max}}$, movement frequency, range of $\varphi$, and extent of knee flexion). Thus, we combined both groups for the mediation analysis.

We performed mediation analysis using ordinary least squares path analysis (Hayes, 2013). As diagrammed in Fig. 6, we hypothesized that greater knee flexion ($X$) leads to poorer performance ($Y$; i.e., greater s.d. of $\varphi$ and range of $\varphi$, or lower AMC rate limit) through its effect on the $\Delta \text{freq}$ ($M_1$) and the $f_{\text{max}}$ ($M_2$). 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 i.q.r. of knee angular displacement, the s.d. of $\varphi$, and the range of $\varphi$ 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 $X$ ($p = .087$), we used a parallel multiple mediator model. The results are summarized in Table S1 (electronic supplementary material).

The results for s.d. of $\phi$ were as follows. Participants who flexed their knees more exhibited a greater frequency reduction (a smaller $\Delta freq$) ($a_1 = .010$), and participants whose frequency reduction was larger exhibited poorer performance (i.e., a greater s.d. of $\phi$; $b_1 = -103.752$). A bias-corrected bootstrap confidence interval that was calculated for the indirect effect ($a_1 b_1 = -0.983$) using 10,000 bootstrap samples lay entirely below zero ($-2.170$ to $-2.294$), which provides evidence of an indirect effect of the extent of knee flexion on performance through $\Delta freq$ ($M_1$). The direct effect of the extent of knee flexion on this performance measure was not significant ($c' = -0.210$, $p = .692$). This means that the extent of knee flexion did not affect performance (i.e., the s.d. of $\phi$) independently of the mediator ($M_1$).

The results for range of $\phi$ were as follows. Participants who flexed their knees more showed a greater frequency reduction (a smaller $\Delta freq$) ($a_1 = .010$) and lower $f_{max}$ ($a_2 = .023$), and participants whose frequency reduction was larger exhibited poorer performance (i.e., a larger range of $\phi$; $b_1 = -3073.791$). Additionally, participants whose $f_{max}$ was lower exhibited poorer performance (i.e., larger range of $\phi$; $b_2 = -786.442$). Bias-corrected bootstrap confidence intervals calculated for the indirect effects ($a_1 b_1 = -29.120$ and $a_2 b_2 = -18.294$, 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 $\Delta freq$ ($M_1$) and $f_{max}$ ($M_2$). The direct effect of the extent of knee flexion on this performance measure was not significant ($c' = 7.733$, $p = .419$). This means that the extent of knee flexion did not affect performance (i.e., the range of $\phi$) 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 $\Delta freq$ ($M_1$) or $f_{max}$ ($M_2$). Bias-corrected bootstrap confidence intervals that were calculated for the indirect effects ($a_1 b_1 = .016$ and $a_2 b_2 = .002$, respectively) using 10,000 bootstrap samples included zero ($-.022$ to $.048$ and $-.015$ to $.030$, respectively). The direct effect of the extent of knee flexion on this performance measure was not significant ($c' = .024$, $p = .159$). 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, nor direct effects for the three performance measures. These results indicate the existence of a directed causal flow from $X$ to $Y$ through mediators.

**DISCUSSION**

We investigated whether the upper rate limit of 1:1 AMC is due to either the biomechanical rate limit or 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 $\Delta freq$ 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—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; Miura et al., 2013a; Miura et al., 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, should be expected to be common (Miura et al., 2016; Miura et al., 2013a; Miura et al., 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 should investigate how he is able to retain AMC at higher frequencies after long-term practice of street dance. One possibility is that we would find 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; Miura et al., 2013a; Miura et al., 2011). Carson et al. (2009) demonstrated that this is due to the effect of gravity by manipulating the effect of gravity using a robotic device. Similarly,
gravity seems to act as a constraint on AMC in sea lion. In Cook et al.’s study (2013), the sea lion shows tempo flexibility, and can synchronise vertical bobbing movement to the beat at different frequencies. The noteworthy result is that a down-on-the-beat pattern emerges 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 movement would lead to further 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; Miura et al., 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 in 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 than in 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 enables 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 for statistical analysis.

Competing interests

No competing interests declared.

Authors’ contributions

AM, KK, and KN conceived and designed the experiments. AM performed the experiments. AM, SF, and MO analysed the data. All authors contributed to and have approved the final manuscript.

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 AM (No.23-9480 and No.25-6687), and by financial aid from Advanced Research Center for Human Sciences, Waseda University to AM 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).
References


Fig. 1. Calculation method for $\Delta f_{\text{req}}$. This figure shows movement frequency as a function of beat frequency for a non-dancer with the greatest frequency reduction (i.e., the smallest $\Delta f_{\text{req}}$) among all the participants. $\Delta f_{\text{req}}$ was the frequency difference between the movement frequency and the smaller value of the $f_{\text{max}}$ and the beat frequency. The dashed line indicates $\Delta f_{\text{req}}$. When the movement frequency is smaller than the beat frequency or the $f_{\text{max}}$, the polarity of $\Delta f_{\text{req}}$ had a negative value. A $\Delta f_{\text{req}}$ less than 0 indicated that movement frequency was reduced in comparison to beat frequency, even though the participant could oscillate at a higher frequency. A $\Delta f_{\text{req}}$ of 0 indicated that when the movement frequency was reduced relative to the beat frequency, this was only as a result of the $f_{\text{max}}$. 
Fig. 2. (A) AMC rate limit and maximum movement frequency by group, and (B) movement frequency as calculated by autocorrelation function. Group mean±s.d. ($N=10$ for Non-dancers, $N=7$ for Dancers). Only the Non-dancers showed significant difference between AMC rate limit and maximum movement frequency (Bonferroni-corrected $p = .001$) (A). We found an almost significant main effect of group using a two-way ANOVA performed on movement frequency ($p = .08$) (B). This implies that the movement frequency tended to differ between the groups.
Fig. 3. Relative frequency of the phase angle of beat time (A) in Non-dancers (N=10) and (B) in Dancers (N=7). The Non-dancers showed a greater extent of phase wandering for a wide range of beat frequencies, whereas the Dancers did not.
Fig. 4. (A) s.d. and (B) range of the phase angle of beat time. Group mean±s.d. (N=10 for Non-dancers, N=7 for Dancers). A two-way ANOVA performed on the s.d. of the phase angle revealed a significant main effect of group (p = .001). The range of the phase angle did not differ between the groups (p = .116).
Fig. 5. (A) Median and (B) i.q.r. of knee angular displacement. Group mean±s.d. (N=10 for Non-dancers, N=7 for Dancers). A two-way ANOVA performed on the median revealed an almost significant main effect of group (p = .061). This implies that the Non-dancers tended to flex their knees more during the task. The i.q.r. did not differ between the groups (p = .925).
Three separate mediation analyses were conducted for three performance measures (Y: s.d. of $\phi$, range of $\phi$, or AMC rate limit).

In all mediation analysis, $X$ is the extent of knee flexion, $M_1$ is $\Delta$freq, and $M_2$ is $f_{\text{max}}$. 

**Fig. 6. Diagram of mediation analysis.**
Supplementary materials

Fig. S1. The first peak value of the autocorrelation function (ACF). Group mean ±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, $F(3.263, 48.943) = 1.403, p = .252, \eta^2_p = .086$. No significant main effect of group was found, $F(1, 15) = .075, p = .787, \eta^2_p = .005$. 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, $F(3.263, 48.943) = 6.590, p = .001, \eta^2_p = .305$. 
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 $\varphi$ and the range of $\varphi$, 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 ($Y$).