Experimental Brain Research (2019) 237:1745–1757
https://doi.org/10.1007/s00221-019-05548-5

RESEARCH ARTICLE

Neuromechanical control of leg length and orientation in children and adults during single-leg hopping

Matthew Beerse[1] · **Jianhua Wu**[2]

Received: 6 December 2018 / Accepted: 24 April 2019 / Published online: 27 April 2019

Abstract

Adult-like fine control of cyclical motor patterns found in locomotion develops into adolescence. Single-leg hopping in place is one such motor pattern where children have demonstrated a reduced capacity to control horizontal motion and match metronome cues. These developmental differences might arise from immature inter-segment coordination strategies and variability regulation. Therefore, the purpose of this study was to use an uncontrolled manifold (UCM) analysis to evaluate the control of segment angle variance (i.e., local variables) to stabilize leg length and leg orientation (i.e., task variables) in the sagittal plane between young adults and children aged 5–11 years old while hopping at different frequencies. The UCM space and its orthogonal space were constructed and segment angle variance was partitioned into these two spaces. Increased variance in the UCM space represents the stabilization of a task variable, while increased variance in its orthogonal space indicates a greater deviation of a task variable from its mean value. Our results indicated that children have developed an adult-like inter-segment coordination strategy of stabilizing leg length at mid-stance and leg orientation during flight. However, children might have an underdeveloped capacity to modulate leg length at take-off from cycle-to-cycle. Moreover, when increasing hopping frequency, children showed limited capacity to selectively increase leg-length stabilization. When decreasing hopping frequency, children illustrated an increased stabilization of leg orientation over the entire stance phase. Mid-stance leg-length stabilization might emerge with the motor skill; however, other inter-segment coordination strategies might continue to develop beyond 11-years of age.

Keywords Uncontrolled manifold analysis · Inter-segment coordination · Segment angle · Development · Locomotion · Variability

Introduction

Locomotion development often progresses through multiple stages, over many repetitions, to fine-tune movement coordination before achieving an adult pattern. For example, children at the age of 4–5 years old are considered mature in certain aspects of the walking pattern, such as step factor and cadence (Sutherland 1997). However, more complex patterns such as coordination of the foot, shank, and thigh elevation angles are still developing until after the age of 12 years old (Cheron et al. 2001). Hopping in place provides another excellent example where children aged 5–11 years old exhibited some adult-like qualities of whole-body vertical stiffness control and frequency modulation, but greater horizontal movement and reduced capacity to hop at a slower than preferred frequency (Beerse and Wu 2016, 2017, 2018). This deviation from adult-like performance might arise from underdeveloped coordination control. Hopping in place has been shown to be an ideal motor pattern to study inter-segment coordination strategies (Ferris et al. 2006; Chang et al. 2008). Moreover, coordination strategies for hopping in place could be applied to other spring-mass model movements, such as running (Farley et al. 1991; Farley and González 1996). Therefore, the evaluation of coordination control following the emergence of the hopping

---

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00221-019-05548-5) contains supplementary material, which is available to authorized users.

✉ Jianhua Wu
jwu11@gsu.edu

[1] Department of Health and Sport Science, University of Dayton, Dayton, OH, USA

[2] Department of Kinesiology and Health, Center for Movement and Rehabilitation Research, Georgia State University, 125 Decatur Street, Atlanta, GA 30302, USA

motor skill, age 5 (Kakebeeke et al. 2013), through the age at which coordination is most likely still developing, 11 years old for typically developing children (Cheron et al. 2001), is imperative to identify and support children with delayed coordination development.

The classic problem with controlling and coordinating movements is the infinite number of solutions available to accomplish the same end goal. This problem was first defined by Bernstein (Bernstein 1967) and was termed 'motor redundancy' with the perspective that the motor system must regulate the multiple degrees of freedom during movement. However, this problem has since been revisited from an opposite perspective of 'motor abundance' where it was proposed that the redundancy is utilized by the motor system to arrive at a variety of solutions for the same task with the same end goal (Scholz et al. 2000, 2012; Yang et al. 2007; Parsa et al. 2017). Therefore, variations at the joint/segment level might serve to stabilize the movement and ultimately minimize the variance of the task goal. The uncontrolled manifold (UCM) analysis is commonly used to partition the variability at the joint/segment level into two subspaces: (a) variability that does not impact the task variable (goal-equivalent variance, or GEV) and (b) variability that impacts the task variable (non-goal equivalent variance, or NGEV (Scholz and Schöner 1999; Tseng et al. 2002; Black et al. 2007; An et al. 2011). Greater amounts of GEV compared to NGEV suggest that local variability is compensatory to stabilize the task goal (Black et al. 2007). In everyday life, this capacity to compensate enables stable locomotion in the presence of internal or external perturbations (Auyang and Chang 2013).

For limb control, the task variable studied has often been the limb endpoint (Tseng et al. 2002; Yang et al. 2007), which can be represented by a limb length and its orientation. For a range of locomotion modalities, including walking, running, and hopping, the control of leg length and leg orientation by segment angle covariation has been demonstrated (Ivanenko et al. 2007). Moreover, there is some evidence that leg length and leg orientation are represented by neurons in the spinal cord (Bosco and Poppele 2000, 2003; Bosco et al. 2000). Therefore, the control of leg length and orientation, in the sagittal plane, has been previously proposed as task variables controlled by the motor system through segment angle compensations during single-leg hopping (Auyang et al. 2009). It was found that young adults have a distinct and flexible inter-segment coordination control policy such that leg length was stabilized during mid-stance of the hopping cycle and leg orientation was stabilized during flight (Auyang et al. 2009; Auyang and Chang 2013). These instances may correspond to time periods when the task variables were most vulnerable to segment angle variance in adults (Auyang et al. 2009). Children aged 5–11 years old show some adult-like regulation of whole-body vertical stiffness (or quasi-stiffness by Latash and Zatsiorsky's definition, Latash and Zatsiorsky 1993) to change hopping frequency, which is determined in part by the compression of the leg, i.e., leg length (Farley et al. 1991; Lee and Farley 1998; Beerse and Wu 2016). Therefore, it is plausible that children may demonstrate an adult-like inter-segment coordination strategy to regulate leg length. This might suggest that the stabilization of leg length is associated with the emergence of the hopping motor skill. In contrast, the inter-segment coordination control of leg orientation might continue to develop, underlying the increased anterior/posterior motion in children compared to young adults (Beerse and Wu 2017).

Increasing hopping frequency from the subject's preferred frequency increases the demand of the task (Farley et al. 1991), which might increase the required inter-segment coordination to stabilize the task (Holt et al. 1995; Auyang et al. 2009). Hopping at a slower than preferred frequency might be a more challenging task than increasing hopping frequency, because it no longer follows the constraints of a spring-mass model (Farley et al. 1998). Moreover, slow hopping has been shown to challenge frequency matching and horizontal movement control (Beerse and Wu 2016, 2017). However, the control policy to regulate the variability of hopping in place at a frequency slower than preferred has not been studied in young adults nor children.

The purpose of this study was to characterize the inter-segment coordination during single-leg hopping between young adults and children aged 5–11 years old and assess how the control strategies modulate when hopping at frequencies faster and slower than preferred. We hypothesized that children will exhibit greater variance of the task variables, leg length, and leg orientation, as well as greater total variance across the segment angles. Further, we hypothesized that children will demonstrate adult-like levels of stabilization of leg length, but not leg orientation such that leg length will be stabilized at mid-stance. With increasing hopping frequency we hypothesized that children will increase leg-length stabilization similar to young adults. But at a slower-than-preferred frequency, children will be unable to increase stabilization of leg length and leg orientation, as expected in young adults, in response to the high demand of the task.

Methods

Participants

Sixteen young adults and seventeen children aged 5–11 years old participated in this study. Inclusion criteria consisted of the ability to hop on a single-leg for 20 s and no previous musculoskeletal conditions that could be made worse by hopping. This study was approved by the institutional review board at the hosting university. Informed consents were obtained from the adult subjects and parents of the children subjects prior to data collection. Verbal assent was obtained from the children subjects prior to data collection.

Protocol

We collected anthropometric measures including height, body mass, and leg length as measured from the anterior superior iliac spine to the medial condyle of the femur to the medial malleolus of the ankle. We then attached a full-body 35-marker set according to the Vicon Plug-In Gait full-body marker set to each subject (Gutierrez-Farewik et al. 2006; Hellmann et al. 2015). A seven-camera Vicon motion capture system (Oxford, UK) with a sampling rate of 100 Hz captured kinematic data. Subjects hopped on an embedded force plate (AMTI, MA, USA) with a sampling rate of 1000 Hz, which was synchronized to the kinematic data. The ground reaction force data from the force plate identified the beginning of stance and flight phases as the time when ground reaction force crossed a threshold of 10 N. We used a fourth-order zero-lag Butterworth filter with a cutoff frequency of 6 Hz on both kinematic and kinetic data.

The single-leg hopping in place protocol is described in detail elsewhere (Beerse and Wu 2016). First, we calculated the preferred frequency of each subject as the average of three 20-s trials. The subject was instructed to hop at their most comfortable frequency on the force plate with their hands on their hips. The subjects hopped on their dominant foot, which was used to kick a ball on the floor (Auyang et al. 2009). The subject's preferred frequency was then used to set the following four metronome conditions: preferred frequency (preferred), a 20% decrease (slow), a 20% increase (moderate), and a 40% increase (fast) from the preferred frequency. The presentation order of the metronome conditions was randomized across subjects. For each metronome condition, the subject hopped in phase with the metronome for three 20-second trials. Adequate rest was provided between trials to minimize fatigue.

Kinematic analysis

For each subject, the trials of the same frequency condition were stitched together. We extracted each hopping cycle from the trials and time normalized to every 1% of the hopping cycle. We calculated four sagittal plane segment angles (i.e., the foot, shank, thigh, and pelvis) in relation to the horizontal using the kinematic marker position data. We calculated a leg-length vector in the sagittal plane between the toe and the anterior superior iliac spine, as well as the orientation of this vector with respect to the ground. We calculated the mean and standard deviation of segment angle, leg length, and leg when the foot makes contact with the ground, i.e., touchdown. We also calculated the displacement of these variables from touchdown to mid-stance, defined as the instance when the COM is at the lowest point during stance phase. Leg length was normalized by each subject's measured leg length.

UCM analysis

The UCM hypothesis was first outlined by Scholz and Schoner in 1999 (Scholz and Schöner 1999) and is briefly described here. First, a variable is defined that is considered to be controlled by the nervous system to successfully complete the task. As previously proposed by Auyang et al. (Auyang et al. 2009), we designated the leg length and orientation as the two task variables for the success of single-leg hopping in place (Fig. 1). To relate changes in segment angles to the task variables, we used the four segment angles (i.e., the foot, shank, thigh, and pelvis) and their segment lengths to create two geometric models as below,

$$L = \sqrt{\begin{matrix}\left(f \cdot \cos\left(\theta_f\right) + s \cdot \cos\left(\theta_s\right) + t \cdot \cos\left(\theta_t\right) + p \cdot \cos\left(\theta_p\right)\right)^2 \\ + \\ \left(f \cdot \sin\left(\theta_f\right) + s \cdot \sin\left(\theta_s\right) + t \cdot \sin\left(\theta_t\right) + p \cdot \sin\left(\theta_p\right)\right)^2\end{matrix}}, \tag{1}$$

$$O = \tan^{-1}\frac{\left(f \cdot \sin\left(\theta_f\right) + s \cdot \sin\left(\theta_s\right) + t \cdot \sin\left(\theta_t\right) + p \cdot \sin\left(\theta_p\right)\right)}{\left(f \cdot \cos\left(\theta_f\right) + s \cdot \cos\left(\theta_s\right) + t \cdot \cos\left(\theta_t\right) + pv\cos\left(\theta_p\right)\right)}, \tag{2}$$

where L is leg length, O is leg orientation, f is foot segment length, θf is foot segment angle, s is shank segment length, θs is shank segment angle, t is thigh segment length, θt is

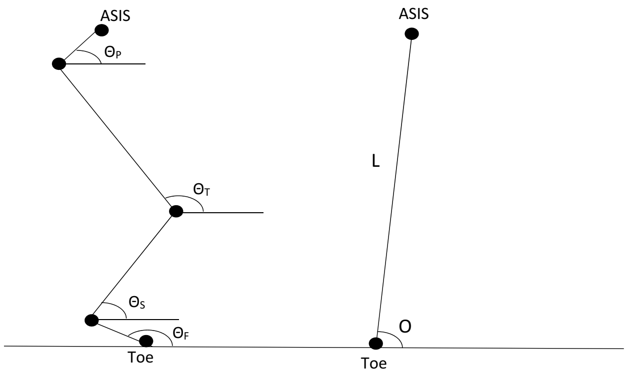

Fig. 1 The kinematic model associated with the uncontrolled manifold analysis. The joint segment angles were measured as the angle between the segment and the horizontal. The leg length (L) was defined as the distance between the anterior superior iliac spine (ASIS) marker and the toe marker placed on the head of the second metatarsal. The leg orientation (O) was the angle between the defined leg and the horizontal

thigh segment angle, p is pelvis segment length, and θp is pelvis segment angle. The geometric models allow for the determination of how the local variable variability contributes to changes of the task variables, leg length and leg orientation. According to the UCM hypothesis, the variability can be partitioned into one of two independent subspaces, an uncontrolled subspace or an orthogonal subspace (Scholz and Schöner 1999). The uncontrolled subspace contains the goal-equivalent variance (GEV) that does not affect the task performance, while the orthogonal subspace contains the non-goal-equivalent variance (NGEV) that deviates the task performance from its mean pattern.

The UCM is a curved space and can be linearized around a reference configuration (Scholz and Schöner 1999). For this study, we normalized each hopping cycle to 100% and completed UCM analyses for every 1% of the cycle. For each UCM analysis we defined a reference configuration as the average segment configurations across all of the hops at that particular time frame. The Jacobian for each geometric model was determined around the reference configuration as the partial derivatives of the model with respect to each of the segment angles (Scholz and Schöner 1999; Scholz et al. 2000; Tseng et al. 2002). Jacobian coefficients function as gains within the model (Yen and Chang 2010). The null space of the Jacobian matrices then defined the UCM,

$$J\left(\theta^{\circ}\right) \cdot \varepsilon = 0, \tag{3}$$

where $J\left(\theta^{\circ}\right)$ is the Jacobian matrix of the reference configuration and ε is the null space. The deviations of the segment angles away from the reference configuration can then be partitioned onto two subspaces: (a) the goal-equivalent deviations that are parallel to the null space and leave the task variable unaffected (Θ_{UCM}) and (b) the non-goal equivalent deviations that are orthogonal to the null space and affect the task variable (θ_{ORT}),

$$\theta_{\text{UCM}} = \sum_{i=1}^{n-d} \varepsilon_i^T \cdot \left(\theta - \theta^{\circ}\right) \cdot \varepsilon_i, \tag{4}$$

$$\theta_{\text{ORT}} = \left(\theta - \theta^{\circ}\right) - \theta_{\text{ORT}}, \tag{5}$$

where n is the number of dimensions in the segment configuration space, and d is the number of dimensions in the task variable (Black et al. 2007; Wu et al. 2009). For our UCM analysis, there were $n = 4$ dimensions in the segment configuration space and $d = 1$ dimension for each task variable. The amount of variability per degree of freedom for GEV and NGEV is estimated as,

$$GEV = \sum \theta_{\text{UCM}}^2 \cdot (n-d)^{-1} \cdot N_{\text{trials}}^{-1}, \tag{6}$$

$$\text{NGEV} = \sum \theta_{\text{ORT}}^2 \cdot d^{-1} \cdot N_{\text{trials}}^{-1}. \tag{7}$$

To control for inter-subject variability we normalized GEV and NGEV by the total amount of variance (TOTV) and calculated an index of motor abundance (IMA) (Tseng et al. 2002; Auyang et al. 2009). The total amount of variance was calculated as the diagonal sum of the covariance matrix per degree of freedom of the four joint segment angles (Yen and Chang 2010),

$$\text{IMA} = \frac{\text{GEV} - \text{NGEV}}{\text{TOTV}}. \tag{8}$$

An IMA greater than zero demonstrates an inter-segment coordination to stabilize the task variable at that particular time. An IMA less than zero indicates an inter-segment coordination to modulate the task variable at that instance and use a greater NGEV for potential task/phase transition (Auyang et al. 2009; Yen et al. 2009; Toney and Chang 2013, 2016). We calculated average IMA over the entire hopping cycle for both task variables. We also partitioned IMA into 10 bins, each containing 10% of the hopping cycle to help visualize the pattern and conduct statistical analysis.

Statistical analysis

Two-way ANOVAs (2 group × 4 frequency) were conducted with repeated measures on frequency on each of the kinematic variables and average IMAs. Two-way ANOVAs (4 frequency × 4 segment) were conducted with repeated measures on both factors on the Jacobian coefficients for each group separately. Normal distribution for each variable was assessed using the Shapiro–Wilk test and the Anderson–Darling test. In cases of non-normal distribution, a log transformation was completed and normal distribution was re-evaluated. Post-hoc pair-wise comparisons were completed with Bonferroni adjustments (group: $\alpha/1$; condition: $\alpha/6$; interaction: $\alpha/28$) when necessary. To determine whether IMA at each 10% of the hopping cycle was significantly different from zero, we conducted two-tailed Student's t tests. All statistical tests were completed using the SAS software (Cary, NC). Significance level was set at $\alpha = 0.05$.

Results

At each condition children hopped significantly faster than adults (Table 1). The kinematic data for one adult subject were inaccurate due to missing hip markers and were removed from analysis. As this study aimed to compare inter-segment coordination between children and adults while hopping at different frequencies, three adult and three children subjects (aged 5, 6, and 7) were removed from data analysis because they did not modify their hopping frequency to the metronome cue. Additionally, three of the remaining children subjects (aged 5, 8, and 8) were unable

Table 1 Mean values (SD) of the subjects' physical characteristics and hopping frequencies

	Physical characteristics					Hopping frequency			
	Gender	Age (years)	Height (m)	Body mass (kg)	Leg length (m)	Slow (Hz)	Preferred (Hz)	Moderate (Hz)	Fast (Hz)
Adults	8M/5F	24.33 (3.60)	1.70 (0.11)	78.08 (16.14)	0.94 (0.07)	1.57 (0.29)	1.96 (0.34)	2.32 (0.38)	2.66 (0.45)
Children	9 M/5F	8.84* (1.75)	1.34* (0.08)	32.97* (7.95)	0.71* (0.05)	2.05* (0.23)	2.56* (0.30)	3.07* (0.36)	3.45* (0.33)

Note that the symbol * denotes that children were significantly different from adults at $p < 0.05$

to complete the fast condition due to an elevated preferred hopping frequency. One of the remaining young adult subjects hopped with a pattern at the slow condition that was opposite the rest of the young adults and skewed the group pattern. These conditions were removed for these subjects, but the remainder of their data were retained for analysis.

Task and local variables

Children exhibited a similar kinematic pattern of the sagittal plane leg vector and segment angles over the course of a hopping cycle compared to young adults (Fig. 2 and Supplemental Table 1). The leg length shortened from touchdown

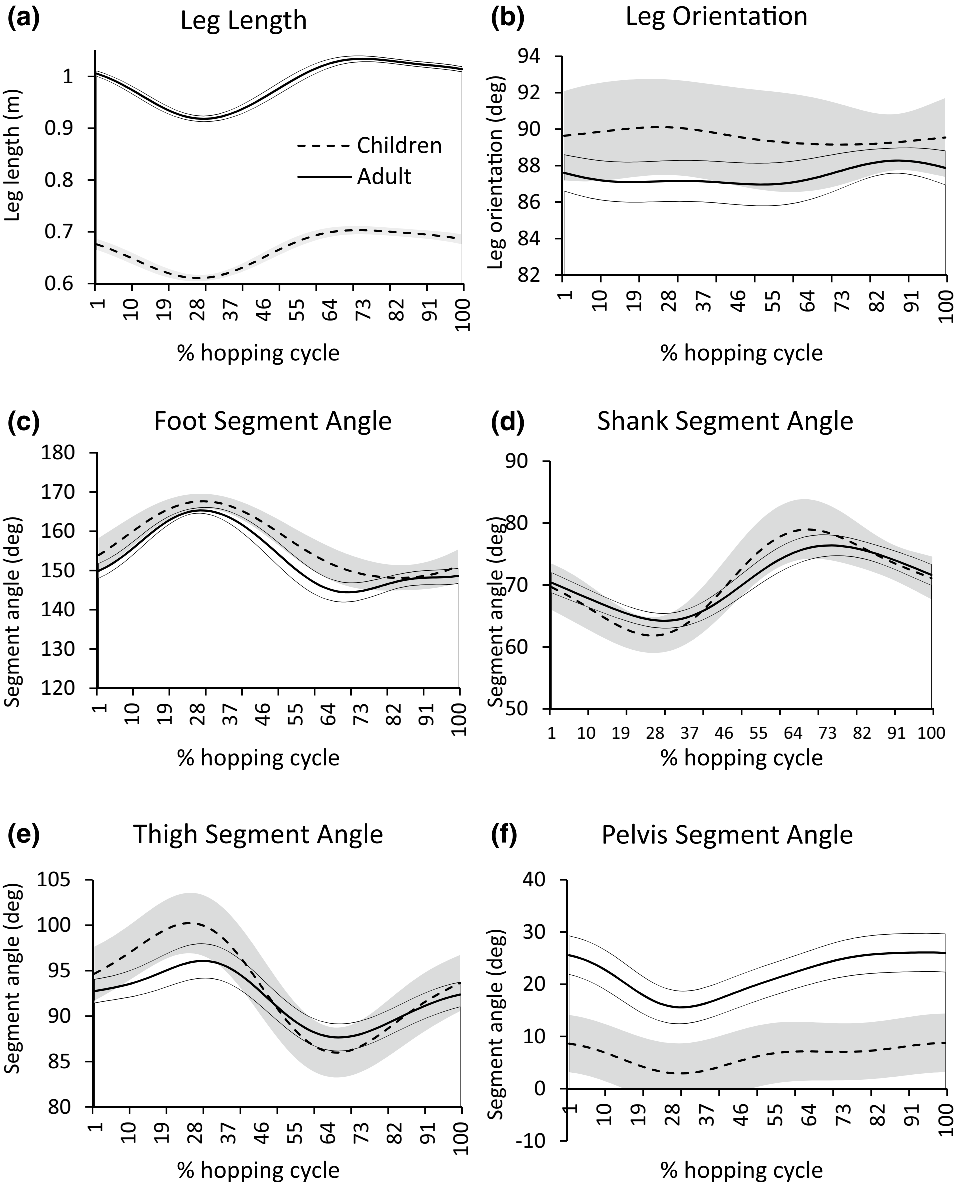

Fig. 2 Mean and standard deviation trajectories of the task variables: **a** leg length and **b** leg orientation, as well as local variables: **c** foot segment angle, **d** shank segment angle, **e** thigh segment angle, and **f** pelvis segment angle over a time-normalized hopping cycle, taken from a single representative adult subject and child subject while hopping at the metronome-cued preferred frequency. ± 1 standard deviation is represented by the solid black lines above and below the average adult trajectory for adults and the grey bands around the average child trajectory for children. Take-off occurs around 70% of the hopping cycle

to mid-stance and lengthened again until flight, where it was mostly maintained until the next touchdown (Fig. 2a). Accompanying the shortening of leg length was rotation of each of the four leg segments, foot, shank, thigh, and pelvis, towards a more horizontal orientation. For leg orientation, children showed a similar pattern compared to adults; however, the orientation angle was more vertical in children compared to adults across the entire hopping cycle (Fig. 2b).

Children hopped with greater variance of the task variables, leg length and leg orientation (Fig. 2), and local variables, segment angles (Fig. 3). Children had greater average leg-length variance over the entire hopping cycle than young adults, and both children and young adults reduced leg-length variance with frequency (Fig. 4a). Statistical analysis revealed that there was a group main effect [$F(1,23) = 8.31$, $p = 0.008$] and a frequency main effect [$F(3,64) = 9.15$), $p < 0.001$]. Post-hoc analysis found that both groups had greater leg-length variance during the slow condition compared to all others. Similarly, children had greater leg-orientation variance over the entire hopping cycle than young adults, and both groups reduced leg orientation variance with frequency (Fig. 4b). Statistical analysis reported that there was a group main effect [$F(1,23) = 65.49$, $p < 0.001$] and a frequency main effect [$F(3,64) = 3.98$, $p = 0.012$]. Post-hoc analysis indicated that both groups had greater leg-orientation variance during the slow condition compared to the moderate condition. The total segment angle variance demonstrated only a group main effect [$F(1,23) = 23.85$, $p < 0.001$] (Fig. 4c), where children had greater local segment angle variance across all conditions compared to young adults.

Comparison of the Jacobian coefficients, highlights a different pattern of segment contributions on the control of leg length between young adults and children but a similar pattern on the control of leg orientation (Fig. 5). For leg length, there was a frequency by segment interaction [$F(9,95) = 2.95$, $p = 0.004$] in young adults (Fig. 5a) and a frequency main effect [$F(3,32) = 4.74$, $p = 0.008$] and a segment main effect [$F(3,36) = 720.26$, $p < 0.001$] (Fig. 5b) in children. Post-hoc analysis indicated that for children, the gains decreased from the slow to moderate and fast frequencies. Moreover, the foot segment had the greatest gain, then the shank, followed by the pelvis, with the thigh having the smallest gain in children. In contrast, young adults demonstrated no significant difference of gain between the foot and shank segment, and between the thigh and pelvis segment. Rather, the foot and shank segment were greater than the thigh and pelvis segment across all frequencies. For leg orientation, young adults demonstrated a frequency by segment interaction [$F(9,96) = 5.13$, $p < 0.001$] (Fig. 5c) and children illustrated a segment main effect [$F(3,36) = 8923.17$, $p < 0.001$] (Fig. 5d). Both groups demonstrated a compete separation of segment gains with the thigh greater than the shank, which was greater than the foot, which was greater than the pelvis.

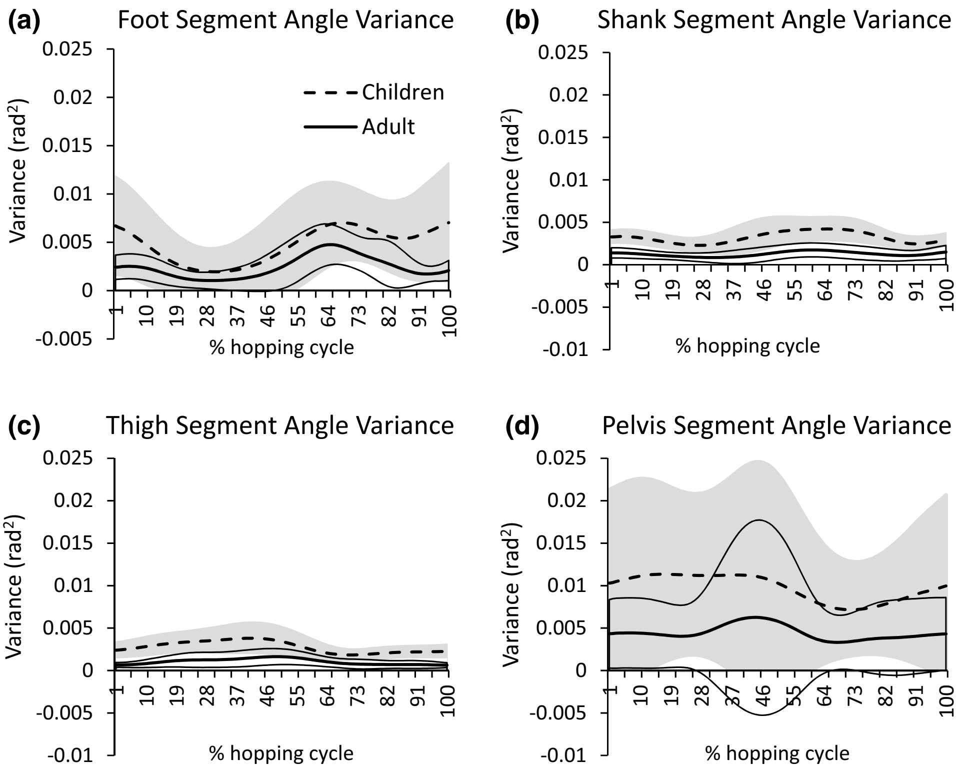

Fig. 3 Mean and standard deviation trajectories of the local variables: **a** variance of foot segment angle, **b** variance of shank segment angle, **c** variance of thigh segment angle, and **d** variance of pelvis segment angle across the hopping cycle during the preferred hopping condition. Take-off occurs for both groups around 70% of the hopping cycle. ± 1 standard deviation is represented by the solid black lines above and below the average adult trajectory for adults and the grey bands around the average child trajectory for children

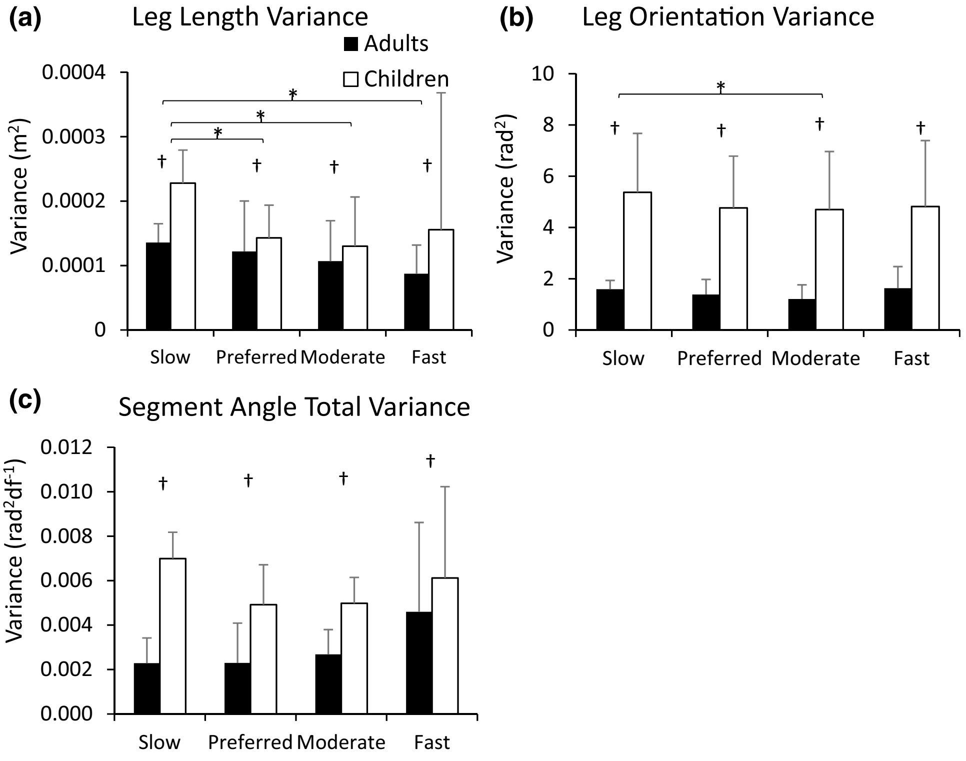

Fig. 4 Mean and standard deviation of variance of the task variables and local variables across the entire hopping cycle. **a** Variance of leg length, **b** variance of leg orientation, and **c** total variance across all four segment angles, i.e., foot, shank, thigh, and pelvis. Symbol † indicates a group effect and * indicates a frequency effect for both groups at $p < 0.05$

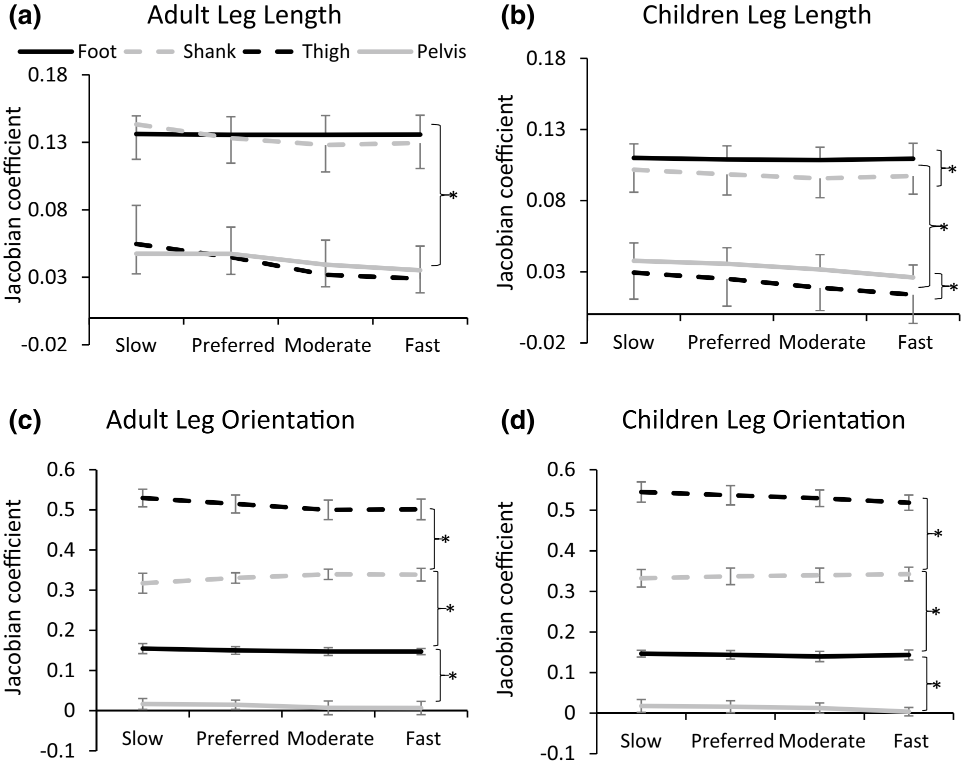

Fig. 5 Mean and standard deviation of the Jacobian coefficients for the leg length (**a**, **b**) and leg orientation (**c**, **d**) models for each group separately. The coefficients represent the influence of each segment on the task variable. For young adults, there was not a difference between the foot and shank segments, nor the thigh and pelvis segments for the leg-length model (**a**). For children, the foot was greater than the shank, which was greater than the pelvis, which was greater than the thigh for the leg-length model (**b**). Adults and children demonstrated a similar pattern for leg orientation (**c**, **d**) where the thigh was greater than the shank, which was greater than the foot, which was greater than the pelvis. * indicates a segment difference across all frequencies at $p < 0.05$

For young adults the Jacobian coefficients for the thigh segment decreased from slow to moderate and fast.

UCM analysis across the hopping cycle

A similar pattern of leg-length stabilization was found between the two groups, but young adults illustrated a distinct leg orientation stabilization pattern compared to children (Fig. 6). Average leg-length IMA across the entire hopping cycle demonstrated a frequency main effect across both groups [$F(3,64) = 15.59$, $p < 0.001$] (Fig. 6a), where IMA increased from slow to moderate, slow to fast, preferred to fast, and moderate to fast. Average leg orientation IMA across the hopping cycle demonstrated a group by frequency interaction [$F(3,64) = 4.72$, $p = 0.005$] (Fig. 6b). Post-hoc analysis indicated that only young adults increased IMA from slow to preferred, moderate, and fast.

UCM analysis time series

IMA at each 10% of the hopping cycle for leg length and leg orientation are illustrated in Figs. 7 and 8, respectively. At each frequency condition, children mostly coordinated their segment angles similar to young adults to hop in place. Specifically, both groups demonstrated an out-of-phase pattern between leg-length and leg-orientation IMA at mid-stance when leg-length IMA is at a peak (Fig. 7) and leg orientation is at a valley (Fig. 8). However, there were differences between groups comparing when IMA was different from

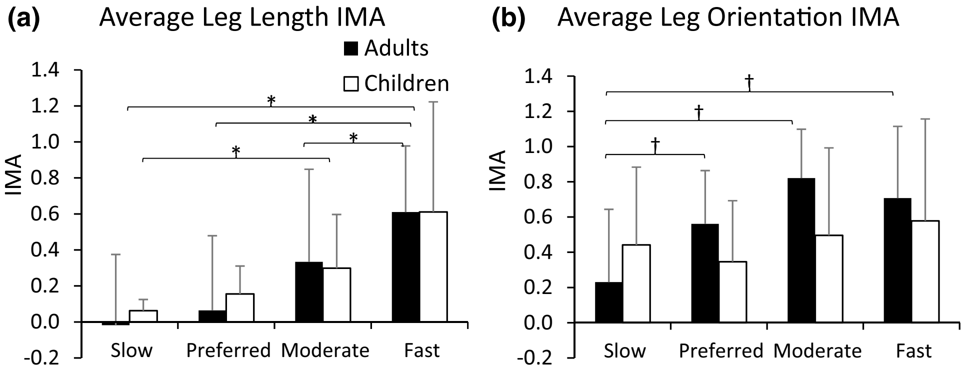

Fig. 6 Mean and standard deviation of index of motor abundance (IMA) across the entire hopping cycle for **a** leg length and **b** leg orientation. Symbol * indicates a frequency difference for both groups and † indicates frequency difference for only adults at $p < 0.05$

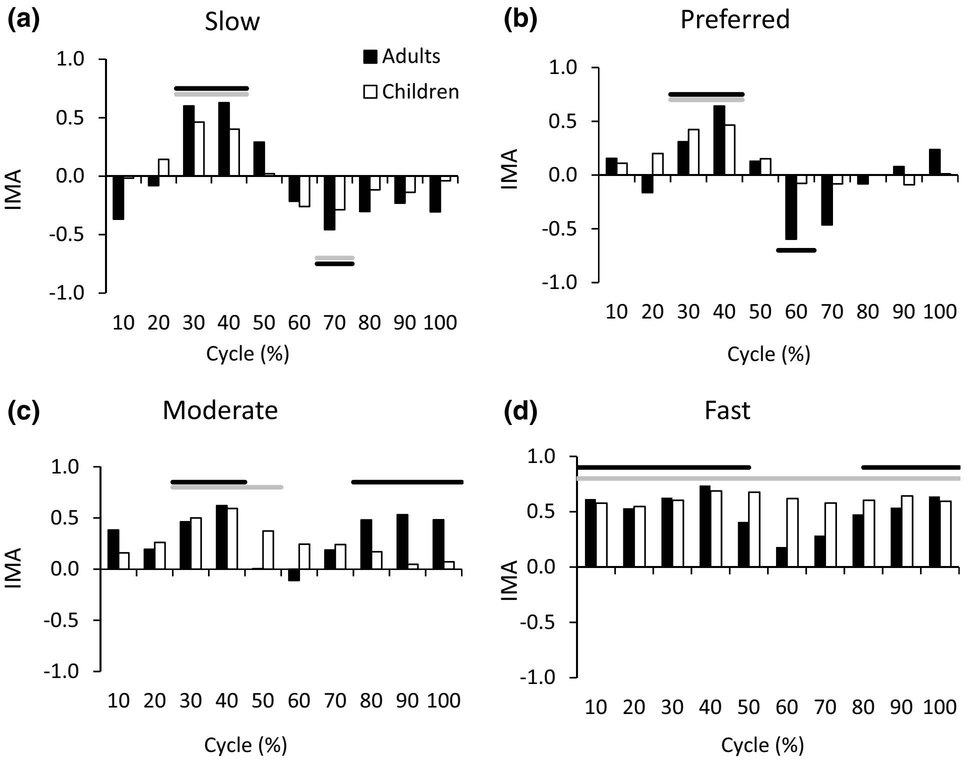

Fig. 7 Mean leg-length IMA values for each of the 10% bins across the hopping cycle. IMA is presented for the slow condition (**a**), preferred condition (**b**), moderate condition (**c**), and fast condition (**d**). The horizontal bars indicate a significant difference from 0 from the independent *t* tests for the adults (black bar) and children (grey bar). Take-off occurred for both groups around 70% of the hopping cycle. For young adults hopping at the slow condition, take-off occurred around 80% of the hopping cycle

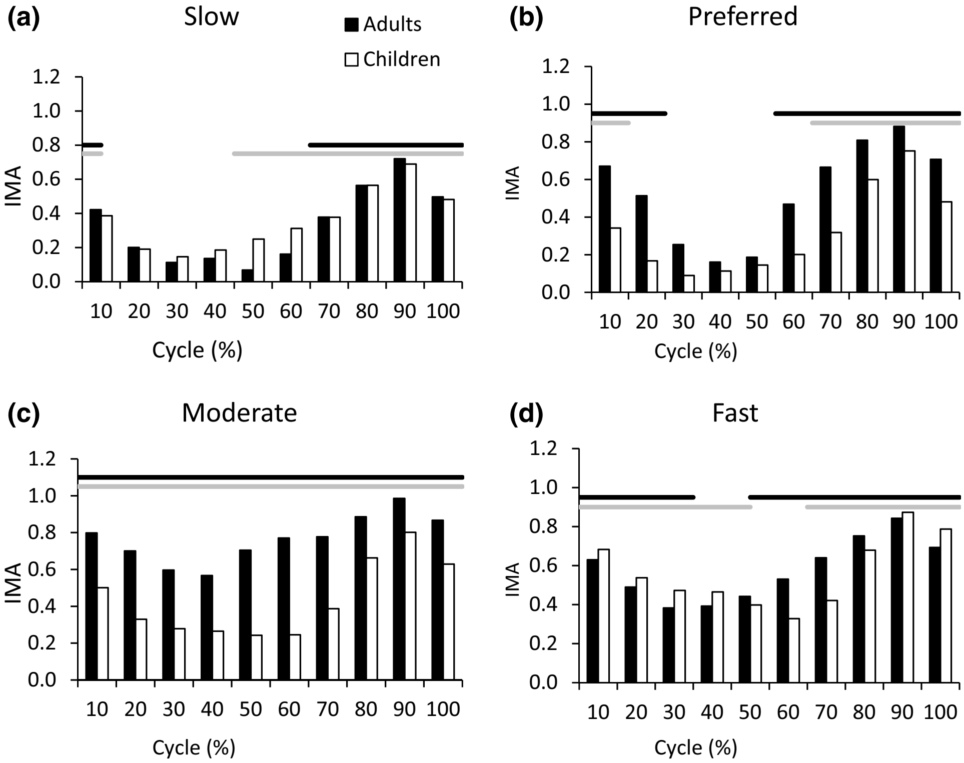

Fig. 8 Mean leg-orientation IMA values for each of the 10% bins across the hopping cycle. IMA is presented for the slow condition (**a**), preferred condition (**b**), moderate condition (**c**), and fast condition (**d**). The horizontal bars indicate a significant difference from 0 from the independent *t* tests for the adults (black bar) and children (grey bar). Take-off occurred for both groups around 70% of the hopping cycle. For young adults hopping at the slow condition, take-off occurred around 80% of the hopping cycle

zero. Notably, for the leg-length IMA pattern, young adults illustrated a leg-length IMA less than zero around take-off during hopping at the *preferred* frequency while children did not (Fig. 7b). Also young adults had a leg-length IMA greater than zero during the flight phase of the *moderate* condition, but children did not until the *fast* condition (Fig. 7c, d). Further, children hopped with a leg-length IMA greater than zero for the entirety of the hopping cycle during the *fast* condition, while young adults preserved their coordination strategy with peak IMA at mid-stance, which decreased around take-off (Fig. 7d). For the leg orientation IMA pattern, children had a leg orientation IMA greater than zero following mid-stance during the *slow* condition, while young adults showed this pattern closer to take-off (Fig. 8a). Further, young adults hopped with a similar leg orientation pattern during the *fast* condition, where IMA was not greater than zero at mid-stance (Fig. 8d).

Discussion

The goal of this study was to assess the inter-segment coordination strategies during single-leg hopping to increase or decrease hopping frequency from preferred in children aged 5–11 years old compared to young adults. Consistent with most of our hypotheses, children hopped with greater leg length, leg orientation, and segment angle variance, and illustrated somewhat adult-like stabilization of leg length at mid-stance. However, children also demonstrated different leg-length and -orientation IMA patterns, particularly at the slow and fast conditions. For frequencies slower than preferred, children increased leg orientation stabilization but not young adults. For frequencies faster than preferred, children could not selectively increase leg-length stabilization during flight phase, but rather increased stabilization throughout the hopping cycle. Our results suggested that the inter-segment coordination strategies for both leg-length and leg orientation are still developing in children beyond 11 years of age.

Variance structure for preferred hopping

While children illustrated a similar kinematic pattern, they hopped with greater task variability and local variability than young adults. Further, children had similar average IMA values for leg length and leg orientation across the hopping cycle at the *preferred* condition. Additionally, the out-of-phase relationship between leg length and leg orientation previously identified in young adults (Auyang et al. 2009), was also found for children. Specifically, leg-length stabilization was prioritized during mid-stance and leg orientation stabilization was prioritized during flight. All of these results suggest that despite having greater variability in both task and local variables, children between the ages of 5–11 years old have developed an adult-like capacity of variability regulation to minimize the variance of local segment angles during critical time periods within a hopping cycle that could disrupt the regulation of leg length and leg orientation (Farley et al. 1991; Auyang et al. 2009).

While the child pattern of leg orientation stabilization closely mimics the adult pattern, a distinct difference was found for leg length around take-off. For young adults, leg length-IMA was less than zero just before take-off. An IMA value less than zero might suggest that the locomotor system no longer prioritizes control of that task variable, i.e., leg length (Tseng et al. 2002), alleviating resources to minimize variance impacting leg orientation. However, the children group did not illustrate a leg-length IMA less than zero and still demonstrated the capacity to stabilize leg orientation during take-off. This suggests that there may not be a need to increase resource availability for the motor system during take-off. Another interpretation of an IMA value less than zero proposes the presence of an active strategy to modulate the task variable through local variability to stabilize an alternative task variable (Yen et al. 2009; Toney and Chang 2013, 2016). For example, during single-leg hopping, the influence of ankle, knee, and hip joint torque variance on anterior/posterior ground reaction force demonstrated an IMA value less than zero at the beginning and ending of stance phase (Yen et al. 2009). This finding was interpreted as cycle-to-cycle adjustments to hop back and forth and maintain an average in-place location. Also, Toney and Chang (2013, 2016) demonstrated that at the time period of step transitions during treadmill walking, the ankle, knee, and hip joint torques were modulated to adjust the anterior/posterior ground reaction force and leg force to maintain consistent center-of-mass accelerations and leg power, respectively (Toney and Chang 2013, 2016). Therefore, we propose that young adults may actively adjust local segment angle variance from cycle-to-cycle to vary leg length at take-off, a time period of transition from stance to flight.

The utility of this strategy may improve the hopping performance, specifically matching the metronome cue. Young adults are often proficient at matching a metronome cue during single-leg hopping in place (Beerse and Wu 2016). After take-off occurs, an individual has minimal impact on their trajectory or the time they spend in flight. Therefore, adjustments to the flight pattern must occur before take-off. For leg length, the foot and shank segment had the greatest influence on leg length within the Jacobian and were not different from each other (Fig. 5a). Therefore, it is likely that the net motion of these two segments, which can be described by ankle joint motion, modified leg length on a cycle-to-cycle basis. Moreover, peak foot and shank segment angle variance occurred around take-off, facilitating the transition from stance to flight (Fig. 3a, b). The ankle joint has already been shown to be the primary joint young adults utilize to adjust leg stiffness to increase hopping frequency and adapt to different surfaces (Farley et al. 1998; Farley and Morgenroth 1999). Therefore, it is plausible that the ankle joint also plays a critical role in frequency matching during single-leg hopping in place. However, to better define the underlying mechanism of this potential active modulation strategy in young adults, a future study should determine the role of individual segment variance and covariance across segments on leg-length stabilization (Yen and Chang 2010).

Control strategy for increasing hopping frequency from preferred frequency

Hopping at frequencies faster than preferred is thought to increase the demand of the task (Holt et al. 1995; Auyang et al. 2009). For both groups, hopping at these faster-than-preferred frequencies did not increase the variance of their global task variables nor the total segment angle variance. However, both groups increased average leg-length IMA at the moderate and fast conditions. These results agree with what has previously been found for young adults, where average leg-length IMA increased at faster-than-preferred frequencies (Auyang et al. 2009). Our results support that faster-than-preferred frequencies require increased inter-segment coordination due to a higher task demand (Holt et al. 1995; Auyang et al. 2009). Moreover, children demonstrated the capacity to increase leg-length stabilization through inter-segment coordination when tasked with hopping at frequencies greater than preferred.

A slightly different pattern emerged when comparing stabilization of leg length at the moderate and fast frequency conditions over the course of the hopping cycle. For young adults, it appeared that their preferred pattern was, to great extent, preserved at the moderate and fast conditions, but scaled with the demand of the task. Specifically, the leg-length IMA pattern was greater than zero at mid-stance, decreased at take-off, and increased again during flight. The scaling was evident during flight, where leg-length IMA was greater than zero at the moderate and fast conditions. Interestingly, the only consistency across conditions demonstrated by children was a leg-length IMA greater than zero at mid-stance. At the moderate condition, children did not increase leg-length IMA during flight. Children did ultimately increase leg-length IMA during flight at the *fast* condition, but with a concurrent increase of leg-length IMA throughout the entire hopping cycle.

It has previously been proposed that mid-stance is a critical time period for hopping as the joints must transition from flexion to extension and vertical force is stabilized (Farley et al. 1991; Auyang et al. 2009; Yen et al. 2009). Therefore, we argue that the emergence of the hopping motor skill might correspond with an ability to stabilize leg length at mid-stance through inter-segment coordination. However, we did not expect an adult-like leg orientation stabilization pattern in children due to the reduced horizontal control during hopping (Beerse and Wu 2016). Rather, our results suggest that the fine-tuning of the hopping motor skill might involve the capacity to selectively stabilize leg length during other time periods of the hopping cycle, most likely flight phase.

Control strategy for hopping at a frequency slower than preferred

Hopping at frequencies slower than preferred is considered to require increased neural control and increased muscular input to actively push-off during the second half of stance phase following energy absorption (Farley et al. 1991; Riese et al. 2013). Therefore, it is plausible that the task demand increases when hopping slower than preferred. It is thought that when the demand of the task increases there is a concurrent increase of stabilization of the task variables (Holt et al. 1995; Auyang et al. 2009). However, average leg-length and -orientation IMA across the hopping cycle were not different between the *slow* and *preferred* conditions in children. Comparing the pattern of stabilization across the hopping cycle, it is evident that hopping slower than preferred was challenging for the children group, but potentially not so for the young adult group.

For leg length, stabilization still occurred around mid-stance for both groups once more highlighting this as a potentially critical time period to maintain a desired whole-body vertical stiffness (Auyang et al. 2009). Leg-length IMA was less than zero around take-off for both groups. As previously discussed, this might suggest the presence of an active modulation strategy to vary leg length at take-off to match the metronome cue (Toney and Chang 2013, 2016). The presence of this strategy at the slow condition and not the preferred condition in children might suggest a cost associated with the strategy or a shift in task prioritization. The preferred condition is thought to occur at a frequency where metabolic cost is minimal (Farley et al. 1991). Therefore, it is plausible that children have not incorporated this modulation strategy into their preferred hopping frequency due to some metabolic cost. Another possibility is that children became aware of the difference between their movement and the metronome cue at the slow condition. In our previous study, the slow condition resulted in the greatest difference between actual and cued hopping frequency in children, but not young adults (Beerse and Wu 2016). Therefore, children might have increased prioritization of matching the metronome cue at the slow condition compared to the other frequencies. This follows previous studies that have demonstrated the movement variance structure is influenced by the constraints of the task (Auyang et al. 2009; Yen et al. 2009; Auyang and Chang 2013). It is likely that children are still developing their ability to actively modulate leg length at take-off to match the metronome cue, evidenced by their increased inaccuracy at the slow condition (Beerse and Wu 2016).

For leg orientation, children increased stabilization during the stance phase compared to the preferred condition. The preferred pattern of leg orientation stabilization for both groups was an IMA greater than zero around take-off and during flight phase. However, at the slow condition, children stabilized leg orientation for more of the hopping cycle, specifically following mid-stance. This finding follows the expected increased stabilization in response to increased task demand (Holt et al. 1995; Auyang et al. 2009). Therefore, our results might suggest that maintenance of leg orientation is challenged in children during slow hopping illustrated by a control strategy to increase stabilization. This result might explain why children had greater difficulty minimizing their horizontal motion during single-leg hopping in place at frequencies slower than preferred compared to young adults (Beerse and Wu 2016, 2017).

This study has some limitations. First, the selection of leg length and orientation as task variables might ignore other parameters that are important for the performance of single-leg hopping in place. However, considering the previous work highlighting the potential importance of leg-length stabilization on hopping in young adults (Auyang et al. 2009), and the similar findings presented in this study, we believe that leg length is a worthwhile parameter to study. Another limitation of this study was the wide age range of our children subjects. This age range most likely includes varying developmental levels and hopping qualities. However, we attempted to minimize these impacts by assessing whether each subject changed their hopping frequency in response to the metronome cue. Therefore, the results of this study highlight a general motor ability for this age range.

Conclusion

Children aged 5–11 years old demonstrated a similar segment angle variance structure as young adults while hopping at their preferred frequency. Stabilization of leg length during mid-stance might develop early with the emergence of the motor skill. However, a capacity to selectively increase leg-length stabilization in response to increasing hopping frequency might take longer to mature. Additionally, children might have an underdeveloped capacity to modulate their leg length on a cycle-to-cycle basis to improve timing performance. Moreover, hopping at a slower than preferred frequency might be a more demanding task for children due to their reduced balance control and immature inter-segment coordination strategy.

Acknowledgements The authors are thankful to all the participants and their families for their participation in this study.

Author contributions MB contributed to conceptualization; data curation; formal analysis; investigation; methodology; software; validation; visualization; original draft writing; review and editing. JW contributed to conceptualization; data curation; formal analysis; investigation; methodology; project administration; resources; software; supervision; validation; visualization; original draft writing; review and editing.

Compliance with ethical standards

Conflict of interest The authors declare that there was no conflict of interest.

References

An Q, Asama H, Stepp CE, Matsuoka Y (2011) Uncontrolled manifold analysis of standing-up motion for development of an assistance system. In: 2011 IEEE international conference on rehabilitation robotics. IEEE, Zurich, Switzerland, pp 1–5

Auyang AG, Chang Y-H (2013) Effects of a foot placement constraint on use of motor equivalence during human hopping. PLoS One 8:e69429. https://doi.org/10.1371/journal.pone.0069429

Auyang AG, Yen JT, Chang Y-H (2009) Neuromechanical stabilization of leg length and orientation through interjoint compensation during human hopping. Exp Brain Res 192:253–264. https://doi.org/10.1007/s00221-008-1582-7

Beerse M, Wu J (2016) Vertical stiffness and center-of-mass movement in children and adults during single-leg hopping. J Biomech 49:3306–3312. https://doi.org/10.1016/j.jbiomech.2016.08.014

Beerse M, Wu J (2017) Comparison of whole-body vertical stiffness and leg stiffness during single-leg hopping in place in children and adults. J Biomech 56:71–75. https://doi.org/10.1016/j.jbiomech.2017.03.001

Beerse M, Wu J (2018) Vertical stiffness and balance control of two-legged hopping in-place in children with and without Down syndrome. Gait Posture 63:39–45. https://doi.org/10.1016/j.gaitpost.2018.04.026

Bernstein N (1967) The coordination and regulation of movements. Pergamon, Oxford

Black DP, Smith BA, Wu J, Ulrich BD (2007) Uncontrolled manifold analysis of segmental angle variability during walking: preadolescents with and without Down syndrome. Exp Brain Res 183:511–521. https://doi.org/10.1007/s00221-007-1066-1

Bosco G, Poppele RE (2000) Reference frames for spinal proprioception: kinematics based or kinetics based? J Neurophysiol 83:2946–2955. https://doi.org/10.1152/jn.2000.83.5.2946

Bosco G, Poppele RE (2003) Modulation of dorsal spinocerebellar responses to limb movement. II. Effect of sensory input. J Neurophysiol 90:3372–3383. https://doi.org/10.1152/jn.00204.2003

Bosco G, Poppele RE, Eian J (2000) Reference frames for spinal proprioception: limb endpoint based or joint-level based? J Neurophysiol 83:2931–2945. https://doi.org/10.1152/jn.2000.83.5.2931

Chang Y-H, Roiz RA, Auyang AG (2008) Intralimb compensation strategy depends on the nature of joint perturbation in human hopping. J Biomech 41:1832–1839. https://doi.org/10.1016/j.jbiomech.2008.04.006

Cheron G, Bouillot E, Dan B et al (2001) Development of a kinematic coordination pattern in toddler locomotion: planar covariation. Exp Brain Res 137:455–466. https://doi.org/10.1007/s002210000663

Farley CT, González O (1996) Leg stiffness and stride frequency in human running. J Biomech 29:181–186

Farley CT, Morgenroth DC (1999) Leg stiffness primarily depends on ankle stiffness during human hopping. J Biomech 32:267–273

Farley CT, Blickhan R, Saito J, Taylor CR (1991) Hopping frequency in humans: a test of how springs set stride frequency in bouncing gaits. J Appl Physiol 71:2127–2132

Farley CT, Houdijk HHP, Van Strien C, Louie M (1998) Mechanism of leg stiffness adjustment for hopping on surfaces of different stiffnesses. J Appl Physiol 85:1044–1055

Ferris DP, Bohra ZA, Lukos JR, Kinnaird CR (2006) Neuromechanical adaptation to hopping with an elastic ankle-foot orthosis. J Appl Physiol 100:163–170. https://doi.org/10.1152/japplphysiol.00821.2005

Gutierrez-Farewik EM, Bartonek Å, Saraste H (2006) Comparison and evaluation of two common methods to measure center of mass displacement in three dimensions during gai. Hum Mov Sci 25:238–256. https://doi.org/10.1016/J.HUMOV.2005.11.001

Hellmann D, Stein T, Potthast W et al (2015) The effect of force-controlled biting on human posture control. Hum Mov Sci 43:125–137. https://doi.org/10.1016/j.humov.2015.08.009

Holt KG, Jeng SF, Ratcliffe R, Hamill J (1995) Energetic cost and stability during human walking at the preferred stride frequency. J Mot Behav 27:164–178. https://doi.org/10.1080/00222895.1995.9941708

Ivanenko YP, Cappellini G, Dominici N et al (2007) Modular control of limb movements during human locomotion. J Neurosci 27:11149–11161. https://doi.org/10.1523/JNEUROSCI.2644-07.2007

Kakebeeke TH, Caflisch J, Chaouch A et al (2013) Neuromotor development in children. Part 3: motor performance in 3- to 5-year-olds: neuromotor development in preschool children. Dev Med Child Neurol 55:248–256. https://doi.org/10.1111/dmcn.12034

Latash ML, Zatsiorsky VM (1993) Joint stiffness: myth or reality? Hum Mov Sci 12:653–692. https://doi.org/10.1016/0167-9457(93)90010-M

Lee CR, Farley CT (1998) Derminants of the center of mass trajectory in human walking and running. J Exp Biol 201:2935–2944

Parsa B, Zatsiorsky VM, Latash ML (2017) Optimality and stability of intentional and unintentional actions: II. Motor equivalence and structure of variance. Exp Brain Res 235:457–470. https://doi.org/10.1007/s00221-016-4806-2

Riese S, Seyfarth A, Grimmer S (2013) Linear center-of-mass dynamics emerge from non-linear leg-spring properties in human hopping. J Biomech 46:2207–2212. https://doi.org/10.1016/j.jbiomech.2013.06.019

Scholz JP, Schöner G (1999) The uncontrolled manifold concept: identifying control variables for a functional task. Exp Brain Res 126:289–306

Scholz JP, Schoner G et al (2000) Identifying the control structure of multijoint coordination during pistol shooting. Exp Brain Res 135:382–404. https://doi.org/10.1007/s002210000540

Scholz JP, Park E, Jeka JJ et al (2012) How visual information links to multijoint coordination during quiet standing. Exp Brain Res 222:229–239. https://doi.org/10.1007/s00221-012-3210-9

Toney ME, Chang Y-H (2013) Humans robustly adhere to dynamic walking principles by harnessing motor abundance to control forces. Exp Brain Res 231:433–443. https://doi.org/10.1007/s00221-013-3708-9

Toney ME, Chang Y-H (2016) The motor and the brake of the trailing leg in human walking: leg force control through ankle modulation and knee covariance. Exp Brain Res 234:3011–3023. https://doi.org/10.1007/s00221-016-4703-8

Tseng Y, Scholz J, Schöner G (2002) Goal-equivalent joint coordination in pointing: affect of vision and arm dominance. Mot Control 6:183–207

Wu J, McKay S, Angulo-Barroso R (2009) Center of mass control and multi-segment coordination in children during quiet stance. Exp Brain Res 196:329–339. https://doi.org/10.1007/s00221-009-1852-z

Yang J-F, Scholz JP, Latash ML (2007) The role of kinematic redundancy in adaptation of reaching. Exp Brain Res 176:54–69. https://doi.org/10.1007/S00221-006-0602-8

Yen JT, Chang YH (2010) Rate-dependent control strategies stabilize limb forces during human locomotion. J R Soc Interface 7:801–810. https://doi.org/10.1098/rsif.2009.0296

Yen JT, Auyang AG, Chang Y-H (2009) Joint-level kinetic redundancy is exploited to control limb-level forces during human hopping. Exp Brain Res 196:439–451. https://doi.org/10.1007/s00221-009-1868-4