© 2020. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2020) 223, jeb224113. doi:10.1242/jeb.224113

RESEARCH ARTICLE

To walk or to run – a question of movement attractor stability

Peter C. Raffalt[1,2], Jenny A. Kent[2,3], Shane R. Wurdeman[2,4] and Nick Stergiou[2,5,*]

ABSTRACT

During locomotion, humans change gait mode between walking and running as locomotion speed is either increased or decreased. Dynamical systems theory predicts that the self-organization of coordinated motor behaviors dictates the transition from one distinct stable attractor behavior to another distinct attractor behavior (e.g. walk to run or vice versa) as the speed is changed. To evaluate this prediction, the present study investigated the attractor stability of walking and running across a range of speeds evoking both self-selected gait mode and non-self-selected gait mode. Eleven subjects completed treadmill walking for 3 min at 0.89, 1.12, 1.34, 1.56, 1.79, 2.01, 2.24 and 2.46 m s^{-1} and running for 3 min at 1.79, 2.01, 2.24, 2.46, 2.68, 2.91, 3.13 and 3.35 m s^{-1} in randomized order while lower limb joint angles and sacrum displacements was recorded. Attractor stability was quantified by continuous relative phase and deviation phase of lower limb segment angles, and the largest Lyapunov exponent, correlation dimension and movement variability of the sacrum marker displacement and the hip, knee and ankle joint angles. Lower limb attractor stability during walking was maximized at speeds close to the self-selected preferred walking speed and increased during running as speed was increased. Furthermore, lower limb attractor stability was highest at a particular gait mode closest to the corresponding preferred speed, in support of the prediction of dynamical systems theory. This was not the case for the sacrum displacement attractor, suggesting that lower limb attractor behavior provides a more appropriate order parameter compared with sacrum displacement.

KEY WORDS: Locomotion, Dynamical system theory, Dynamics, Coordination, Gait

INTRODUCTION

Gait mode selection

During terrestrial locomotion, bipeds and quadrupeds are able to shift between multiple gait modes, with the transition occurring within a relatively few steps (e.g. from walk to run or trot to gallop). The underlying control mechanisms that evoke the transition between gait modes have been investigated intensively, and several possible driving factors have been discussed in the literature. These involve the minimization of energy expenditure (Hoyt and Taylor, 1981; Hreljac, 1993b; Minetti et al., 1994; Thorstensson and Roberthson, 1987), the mechanical limitation of different gait modes (Alexander, 1977; Hreljac, 1993a, 1995a,b; Kram et al., 1997; Ranisavljev et al., 2014; Thorstensson and Roberthson, 1987), the minimization of mechanical stress (Biewener and Taylor, 1986; Biewener et al., 1983; Farley and Taylor, 1991; Hreljac, 1993a; Taylor, 1985) and the integration of sensory input and centrally controlled rhythmic motor output (Caggiano et al., 2018; Hansen et al., 2017; Kiehn, 2016; Prilutsky and Gregor, 2001; Thorstensson and Roberthson, 1987; Voigt et al., 2019).

These explanations primarily focus on the minimization or optimization of a specific parameter that constitutes the governing mechanism for the transition between gait modes. This suggests that comprehensive computational work is required to determine when it is beneficial to change gait. It also implies that a cost function (e.g. related to energy expenditure, muscular stress or joint forces) dictates the executed movements. However, as an alternative to this, dynamical systems theory suggests that the executed movement originates from a self-organization process creating better coordinated motor behaviors (i.e. the best solution given the constraints on the system and the task at hand) (Kelso et al., 1979). Furthermore, changes in motor behavior occur through phase transition from one stable attractor behavior to another (e.g. walk to run) (Haken et al., 1985; Kelso and Schöner, 1988). These changes can be initiated by alterations in a control parameter (e.g. movement frequency or speed). The behavior of the attractor can be summarized by an order parameter, i.e. a low-dimensional collective variable providing a measure of the organizational state of the system (Haken, 1983).

In their seminal work, Diedrich and Warren (1998, 1995) presented an illustration of the phase transition between two attractors in relation to human locomotion. This transition includes: (1) a qualitative change in the order parameter, (2) a sudden jump in the order parameter as the control parameter is continuously changed, (3) a resistance to change to another basin of attraction as the control parameter is changed; and (4) decreased attractor stability, indicated by an increase in the magnitude of the variability of the order parameter when approaching the transition point. Hence, two different principles can be inferred. First, a 'control parameter-dependent attractor stability principle' would suggest that a change in the control parameter (in this case, locomotion speed) will move the system from one stable attractor (i.e. walking at the preferred walking speed, PWS) through an unstable region before abruptly switching to a different, stable attractor (i.e. running at the preferred running speed, PRS). Second, an 'attractor stability optimization principle' would suggest that the self-selected movement solution at a given speed will exhibit a more stable attractor compared with the alternative movement solution. This means that walking at speeds close to the PWS will exhibit a more stable attractor compared with running at the same speed. Similarly, running at speeds close to the PRS will exhibit a more stable attractor compared with walking at the same speed. To test these two inferred principles experimentally, Diedrich and Warren (1995) recruited healthy individuals to both walk and run at speeds ranging

[1]Department of Physical Performance, Norwegian School of Sport Sciences, Sognsveien 220, 0806 Oslo, Norway. [2]Department of Biomechanics and Center for Research in Human Movement Variability, University of Nebraska at Omaha, 6160 University Drive, Omaha, NE 68182-0860, USA. [3]Department of Physical Medicine and Rehabilitation, Northwestern University, 680 N Lake Shore Dr, Chicago, IL 60601, USA. [4]Department of Clinical and Scientific Affairs, Hanger Clinic, 11155 S. Main St., Houston, TX 77025, USA. [5]College of Public Health, University of Nebraska Medical Center, Omaha, NE 68198-4355, USA.

*Author for correspondence (nstergiou@unomaha.edu)

N.S., 0000-0002-9737-9939

Received 26 February 2020; Accepted 2 June 2020

from below to above the walk-to-run transition speed. The attractor stability was quantified as the variation in the relative phase of the intersegmental lower limb coordination (i.e. the coupling between lower limb joint angles within the same leg; Diedrich and Warren, 1995). In support of the two inferred principles, it was observed that the stability decreased during walking at both low and high walking speeds with a local maximum at intermediate speeds close to PWS, and the stability decreased at low running speeds but increased or remained constant at high running speeds. Furthermore, it was observed that stability was higher during walking at relatively low speeds compared with running at the same speed. The opposite pattern was seen at relatively high speeds but only for the ankle–knee joint coupling (Diedrich and Warren, 1995).

Dynamics of human locomotion

The method applied by Diedrich and Warren (1998, 1995) captures the spatiotemporal configurations of the system by providing a measure of the synchronized oscillatory motion of two coupled segments. However, according to dynamical systems theory, the attractor behavior of the system in question is characterized not only by the spatiotemporal configurations of elements (e.g. coordination of segments across the gait cycle) but also by the temporal development of the spatial configurations, i.e. the dynamics. The latter part addresses how one spatial configuration influences future configurations (e.g. the temporal relationship between subsequent coordination of segments) and has been linked to the underlying motor control strategy (Newell and Corcos, 1993). This feature of dynamical systems is related to the attractor stability (Stergiou, 2004, 2016). Thus, increased attractor stability of a dynamical system is characterized by a high statistical likelihood of the reoccurrence of specific patterns in specific orders whereas decreased attractor stability is characterized by a random structure with low statistical likelihood of repeated patterns. Therefore, we argue that the investigation of stability according to Diedrich and Warren (1998, 1995) is limited. We submit that their methodology of evaluating the attractor's stability through the examination of the variation in the relative phase of the intersegmental lower limb coordination needs to be supplemented with investigation of the temporal dynamics of the interacting components. Considering these limitations in the investigative approach used by Diedrich and Warren (1995), it is crucial, first, to verify their observations using a similar protocol and analytical approach and, second, to confirm that their conclusions hold true when the temporal dynamics is evaluated.

Previous studies have quantified the dynamics in continuous human movements such as walking in order to investigate the underlying motor control strategy (e.g. Chien et al., 2015; England and Granata, 2007; Raffalt et al., 2017). In agreement with the aforementioned principle about control parameter-dependent attractor stability, the presence of a U-shaped relationship between movement dynamics and speed has been observed for both walking (Chien et al., 2015; Raffalt et al., 2017) and running (Jordan et al., 2006). However, the methodological design of these studies did not challenge this attractor stability optimization principle. To do so requires a study protocol that forces the motor control system to solve the locomotion task using an alternative solution to the preferred one. Therefore, the present study included a protocol similar to that of Diedrich and Warren (1995), in which the constraints of the locomotor task are manipulated and the control parameter are scaled, in order to evoke both stable self-selected movement solutions and unstable non-self-selected solutions to the same task. By quantifying the dynamics of these alternative solutions, this alternative protocol permits the attractor stability optimization principle to be challenged in the context of human locomotion. The attractor stability principle optimization would be disproved if the self-selected movement solution at a given speed does not exhibit greater attractor stability compared with the alternative movement solution.

Order parameter identification

When assessing attractor behavior, the identification of an appropriate order parameter is crucial, and a variety of variables have been investigated in relation to human walking and running. These variables include center of mass displacement (Dingwell and Marin, 2006) or acceleration (Raffalt et al., 2017), lower limb joint angles (England and Granata, 2007; Raffalt et al., 2017) and segment angles (Diedrich and Warren, 1995; Kurz et al., 2005; Stergiou et al., 2001). The attractor behavior of center of mass variables (displacement and acceleration) represents the combined influence of all the movements within the system and can be strongly linked to the energy cost of locomotion (Gottschall and Kram, 2003; Grabowski, 2010). In contrast, the attractor behavior of the joint or segment angles originates from the oscillatory movement of the lower limb, and is related to its pendulum-like function during walking and its spring-like function during running (Cavagna and Margaria, 1966; Cavagna et al., 1963). However, to the best of our knowledge, no consensus exists on the selection of an order parameter for human locomotion. By including both center of mass variables and lower limb joint angle-based behavior attractors, the present study sought to clarify which of these variables best captures the movement dynamics of human locomotion.

Study purpose

The purpose of the present study was to investigate the attractor stability of two tasks, walking and running, across speeds, with changed task constraints evoking both stable self-selected movement solutions and unstable non-self-selected movement solutions. To fulfill this purpose, the present study adopted the same experimental and analytical approach as Diedrich and Warren (1995) and, additionally, investigated the stability of the movement attractor through an evaluation of the temporal dynamics. Furthermore, the present study aimed to identify an appropriate order parameter: investigating the response of both center of mass variables and lower limb joint angle variables to alterations in speed and task constraints. The present study included healthy young subjects who walked and ran at speeds below and above their PWS and the PRS. Continuous relative phase was used to quantify the oscillatory motion of the coupled lower limb segments as a measure of the segmental coordination, and the deviation phase was used to assess the stability of the executed coordination pattern. The temporal dynamics of the center of mass displacements and lower limb joint angles was investigated using the largest Lyapunov exponent (LyE) and correlation dimension (CoD). LyE and CoD quantify the exponential rate of divergence or convergence of the attractor's trajectory in state space (Wolf et al., 1985) and the fractal dimension of the attractor in the occupied state space (Grassberger and Procaccia, 1983), respectively. Additionally, movement variability was assessed by the ensemble average standard deviation (meanSD) of the center of mass displacement and lower limb joint angles across the gait cycle.

In agreement with the two principles inferred from Diedrich and Warren (1995), we formulated the following hypotheses: (1) the movement solution during walking at PWS and during running at PRS is a stable behavioral attractor for that particular gait mode while speeds below and above would display significantly different dynamics and (2) at speeds close to the preferred speed of a particular gait mode the movement solution would exhibit a more stable attractor behavior compared to the alternative gait mode at the same speed. When using the relative phase approach, stable attractor behavior would be characterized by a low deviation phase of the thigh-shank coupling and thigh-foot coupling consistent with Diedrich and Warren (1995). When assessing the dynamics of the attractor behavior, stable attractors would be characterized by low values of LyE and CoD and when assessing movement variability, stable attractors would be characterized by a low meanSD.

To evaluate whether a center of mass movement-based or a joint angle-based attractor behavior constitutes the most appropriate order parameter for human locomotion, the present study included 3D kinematic measurements of the sacrum position and sagittal plane hip, knee and ankle joint angles. It could be speculated that the variable(s) confirming the proposed hypotheses would represent the most appropriate order parameter(s).

MATERIALS AND METHODS

The present investigation included analysis of data collected in a previous study (Raffalt et al., 2019). The present and previous study share the same subjects and experimental equipment (motion capture system and treadmill). The present study, however, includes an extended protocol and analyses of unpublished data.

Subjects

Five males and six females (mean±s.d. age: 23.3±3.9 years, body height: 1.74±0.10 m and body mass: 72.1±14.3 kg) were included in the present study. The participants were physically active, familiar with treadmill walking and running and did not report any musculoskeletal injuries or cardiovascular or neurological diseases. All participants were informed of the experimental procedures before giving their written consent to participate in the study. The study was approved by the Institutional Review Board of the University of Nebraska Medical Center and the study was carried out in accordance with the approved protocol.

Experimental setup and procedure

After completing a brief warm-up session on a treadmill, the PWS and PRS of each participant were established using a standardized protocol explained elsewhere (Dingwell and Marin, 2006). Briefly, the participants were blinded to the speed of the treadmill as it was gradually increased and decreased above and below what was reported as comfortable. The average of the speeds reported as comfortable for walking and running was termed the PWS and PRS, respectively. The mean±s.d. of PWS and PRS was 1.26±0.23 m s^{-1} and 2.50±0.34 m s^{-1}, respectively. Following a short rest, the participants were fitted with 15 retro-reflective markers placed bilaterally superficial to the: (1) anterior superior iliac spines, (2) greater trochanters, (3) lateral knees, (4) tibial tubercles, (5) lateral ankles, (6) posterior heels (on shoes) and (7) fifth metatarsal heads, laterally (on shoes). An additional single marker was placed on the sacrum (Vaughan et al., 1992). The participants then completed 8 trials of 3 min walking at 0.89, 1.12, 1.34, 1.56, 1.79, 2.01, 2.24 and 2.46 m s^{-1} and 8 trials of 3 min running at 1.79, 2.01, 2.24, 2.46, 2.68, 2.91, 3.13 and 3.35 m s^{-1} in randomized order of both speed and gait mode. Each trial was separated by at least 2 min rest to avoid fatigue development influencing the performance of the participants. During the walking trials, the participants were instructed to continue to maintain a walk whereby at no point should both feet be off the ground, although the higher speeds might result in discomfort and the urge to start a light jog or run. Maintenance of ground contact with at least one foot at all times was visually confirmed. In case of doubt, vertical ground reaction forces recorded by the treadmill-embedded force platforms were consulted (data not included in the study). During running trials, the participants were instructed to continue to maintain a run whereby at no point should both feet be on the ground and there should be a period where both feet were off the ground, although the lower speeds might result in discomfort and the urge to start walking. During all trials, 3D position data of the 15 markers were continuously recorded at 120 Hz using a system of 12 high-speed cameras (Motion Analysis Corp., Santa Rosa, CA, USA). All subsequent analyses were on kinematic data and the sampling frequency was determined to provide sufficient resolution for toe-off event detection, center of mass displacement, and segment and joint angles.

Data analysis

All analyses were performed using custom-written scripts in Matlab (Mathworks 2011, Inc., Natick, MA, USA).

Continuous relative phase

The marker position data was low-pass filtered at 8 Hz with a zero-phase lag, fourth-order Butterworth filter. Thigh, shank and foot segment angles with respect to the horizontal line in the sagittal plane of the segment were calculated from each trial (Vaughan et al., 1992). An abrupt change in the anterior–posterior (AP) displacement of the right toe marker indicating the change from a backward to a forward motion during the contact phase was identified as toe off of the right foot. Seventy-five strides (i.e. right toe off to the subsequent right toe off) were identified as the minimum number of completed strides across all strides and all subjects. The AP, mediolateral (ML) and vertical (Vert) displacements of the sacrum marker were used as a surrogate of the center of mass displacement and were extracted together with the right hip, knee and ankle joint angles for further analysis.

The procedure to calculate continuous relative phase is described briefly below but further details can be found elsewhere (Hamill et al., 1999; Kurz and Stergiou, 2004; Lamoth et al., 2002). It consisted of four steps. First, each segment angle was time-normalized to the stride phase. Second, a phase plane for each segment was created by plotting the normalized segment velocity as a function of the normalized segment angle following the normalization procedure presented by Hamill et al. (1999). Third, the phase angle was calculated as the angle between the right horizontal and the vector connecting two consecutive pairs of coordinates in each of the four quadrants. Phase angles were calculated for the thigh and shank segment flexion/extension and for foot plantarflexion/dorsiflexion. Finally, the continuous relative phase was calculated for the thigh–shank segment coupling and the thigh–foot segment coupling by subtracting the phase angle of the proximal segment from the phase angle of the distal segment. Continuous relative phase values close to 0 deg indicate in-phase segment coordination and continuous relative phase values close to 180 deg indicate out-of-phase segment coordination. The average continuous relative phase for each subject was calculated by averaging it at each time point across the 75 strides, and deviation phase was calculated as the standard deviation at each time point across all strides. Finally, the mean continuous relative phase and mean deviation phase were calculated by averaging the continuous relative phase and deviation phase across the stride cycle, respectively.

Journal of Experimental Biology (2020) 223, jeb224113. doi:10.1242/jeb.224113

The largest LyE and CoD

The marker position data were not filtered prior to inclusion in the following analyses. Hip, knee and ankle joint angles in the sagittal plane were calculated (Vaughan et al., 1992) for each trial. Before calculating LyE and CoD, the joint angles and sacrum position time series were reconstructed in state space using the method of delay embedding (Sauer and Yorke, 1993; Sauer et al., 1991; Takens, 1981). The time delay (τ) was calculated using the average mutual information algorithm and the embedding dimension (EmD) was calculated using the false nearest neighbor algorithm (Wurdeman, 2016). In agreement with our previous study (Raffalt et al., 2019), the individual τ and EmD for each variable and each trial were used to reconstruct each time series in state space. The LyE was calculated using the algorithm presented by Wolf et al. (1985) and the CoD was calculated using the algorithm presented by Grassberger and Procaccia (1983).

The center of mass displacement variability (i.e. extracted from the sacrum marker position) and joint angle variability were calculated by (1) time-normalizing the time series to 100% of each stride, (2) calculating the standard deviation across all strides for each time point and (3) averaging the standard deviation across all time points (meanSD) (James, 2004).

Statistics

Based on previous studies with similar research question, experimental design and measures (Diedrich and Warren, 1995; Raffalt et al., 2017), it was estimated that a minimum of 10 participants were required to reach significant between-speed and between-gait mode differences of at least 10% with a statistical power of 80% and a significance level of 5%. Because of the inability of a few subjects to walk at the highest speeds and because of technical issues, data were lost from 10 out of the total 176 trials (11 subjects×8 speeds×2 gait modes). To evaluate the first hypothesis, the effect of speed on each dependent variable was assessed for both gait modes using a mixed-model ANOVA for repeated measures with speed as the repeated factor. In the case of an overall effect of speed, a Holm–Šidák *post hoc* test was applied and a quadratic regression analysis was performed to determine the nature of the relationship between speed and the dependent variable in question. The overall percentage of variance accounted for by the regression (r^2) and the *P*-value were determined. To evaluate the second hypothesis, the effect of speed and gait mode on the dependent variables extracted from the four shared speeds (1.79, 2.01, 2.24 and 2.46 m s^{-1}) was assessed using a mixed-model ANOVA with speed and gait mode as the repeated factors. In the case of an overall effect of speed, gait mode and the speed–mode interaction, a Holm–Šidák *post hoc* test was applied. The level of significance was set at 0.05. All statistics were computed in SPSS (IBM SPSS Statistics, version 24, 2016, USA).

RESULTS

Segment coordination and coordination variability

There was a significant effect of speed during both walking and running on the mean average continuous relative phase for the thigh–shank segment coupling (Table 1). At relatively low and high walking speeds, the thigh–shank coupling was more out of phase than at intermediate speeds (Fig. 1A). At low running speeds, the coupling was more out of phase than at higher running speeds. For both tasks, there was a significant curvilinear relationship between speed and relative phase. For the four shared speeds, the segment coordination was more in phase during walking than during running. There was a significant effect of speed during both tasks on the mean average continuous relative phase for the thigh–foot segment coupling (Fig. 1B). For both tasks, the segment coupling changed in a curvilinear fashion towards more in-phase coordination as speed increased.

The coordination variability, assessed by the mean deviation phase, showed a similar pattern for the thigh–shank and thigh–foot segment coupling (Fig. 1C,D). There was a significant curvilinear

Table 1. Effect of speed on attractor behavior stability during walking and running

		Walking		Running	
		F-value	*P*-value	*F*-value	*P*-value
Continuous relative phase	Thigh–shank	5.13	<0.0001	8.81	<0.0001
	Thigh–foot	92.87	<0.0001	7.95	<0.0001
Deviation phase	Thigh–shank	11.09	<0.0001	26.91	<0.0001
	Thigh-foot	16.58	<0.0001	39.04	<0.0001
LyE	Hip joint	14.13	<0.0001	13.34	<0.0001
	Knee joint	18.60	<0.0001	3.64	0.002
	Ankle joint	2.02	NS	2.69	0.015
CoD	Hip joint	8.02	<0.0001	6.34	<0.0001
	Knee joint	13.10	<0.0001	9.98	<0.0001
	Ankle joint	3.24	0.005	6.78	<0.0001
meanSD	Hip joint	26.21	<0.0001	3.41	0.003
	Knee joint	17.96	<0.0001	3.81	0.001
	Ankle joint	14.67	<0.0001	2.91	0.010
LyE	AP	1.855	NS	1.62	NS
	ML	20.18	<0.0001	1.19	NS
	Vert	2.42	0.028	0.884	NS
CoD	AP	0.83	NS	1.61	NS
	ML	5.19	<0.0001	1.59	NS
	Vert	4.17	0.001	1.31	NS
meanSD	AP	1.48	NS	2.94	0.009
	ML	1.47	NS	1.42	NS
	Vert	21.18	<0.0001	3.79	0.001

Results of the one-way mixed-model ANOVA for repeated measures with speed as the independent factor.
LyE, Lyapunov exponent; CoD, correlation dimension; meanSD, movement variability; AP, anterior–posterior; ML, mediolateral; Vert, vertical; NS, not significant.

Journal of Experimental Biology

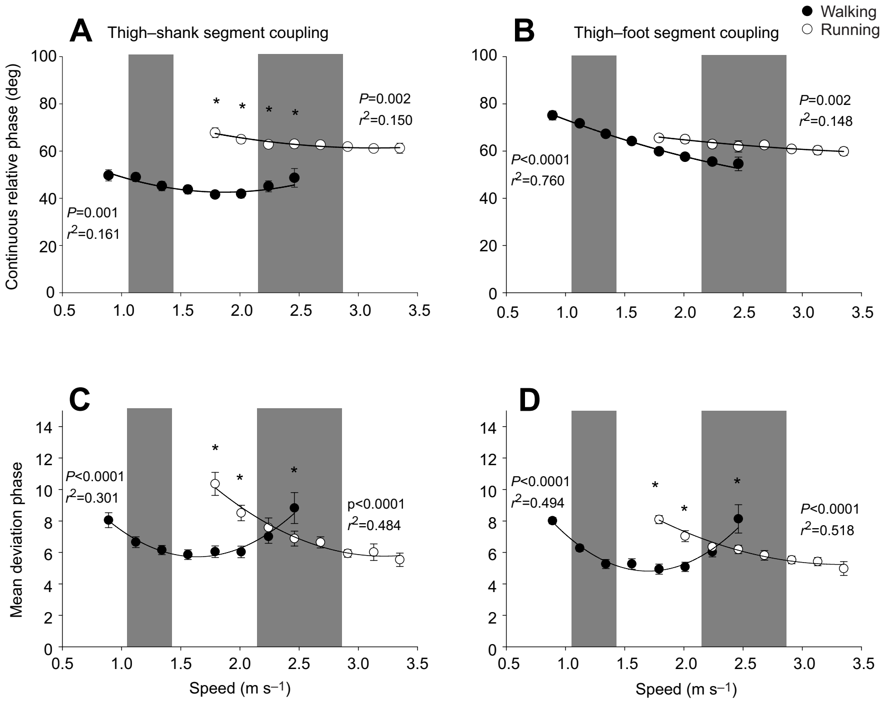

Fig. 1. Mean average continuous relative phase and mean deviation phase. Group (n=11) mean± s.e.m. of the mean average continuous relative phase and mean deviation phase for the thigh–shank (A,C) and thigh–foot (B,D) segment coupling during walking and running. In the case of a significant effect of speed (mixed-model ANOVA for repeated measures, P<0.005) and a significant curvilinear relationship, a regression line is shown. Gray areas indicate the mean±s.d. of preferred walking speed (PWS) and preferred running speed (PRS). *Significant difference in the dependent variable between gait modes (mixed-model ANOVA, P<0.005).

relationship between speed and both couplings during the two tasks. During walking, the relationship was U-shaped, with the lowest mean deviation phase occurring at the intermediate speeds. During running, the mean deviation phase decreased with increasing speed. There was a significant gait mode–speed interaction in the two-way ANOVA (Table 2), and the *post hoc* test revealed that the mean deviation phase was higher during running at low speeds and lower during the highest speed when compared with walking.

Joint angles

There was a significant effect of speed on LyE for the hip and knee joints during walking and for all three joints during running (Table 1). During walking, there was a significant, U-shaped relationship between speed and hip and knee joint LyE, with significantly lower values at the intermediate speed of 1.56 m s^{-1} compared with the lowest and the two highest speeds. During running, the LyE of all three joints decreased significantly in a curvilinear fashion with increasing speed (Fig. 2A–C). The two-

Table 2. Effect of gait mode and speed on attractor behavior stability

		Gait mode		Speed		Mode–speed interaction	
		F-value	*P*-value	*F*-value	*P*-value	*F*-value	*P*-value
Continuous relative phase	Thigh–shank	485.7	<0.0001	0.64	NS	5.43	0.002
	Thigh–foot	98.01	<0.0001	8.56	<0.0001	0.57	NS
Deviation phase	Thigh–shank	40.84	<0.0001	4.89	0.004	34.64	<0.0001
	Thigh–foot	24.56	<0.0001	2.82	0.045	28.92	<0.0001
LyE	Hip joint	23.07	<0.0001	0.80	NS	18.33	<0.0001
	Knee joint	15.79	<0.0001	5.75	0.001	12.77	<0.0001
	Ankle joint	4.77	0.032	0.24	NS	2.87	0.043
CoD	Hip joint	0.12	NS	2.04	NS	1.39	NS
	Knee joint	13.21	0.001	1.20	NS	4.90	0.004
	Ankle joint	1.66	NS	3.59	0.018	2.02	NS
meanSD	Hip joint	0.36	NS	11.97	<0.0001	36.32	<0.0001
	Knee joint	0.001	NS	10.59	<0.0001	22.72	<0.0001
	Ankle joint	6.55	0.013	7.97	<0.0001	21.79	<0.0001
LyE	AP	0.16	NS	0.80	NS	1.03	NS
	ML	1.80	NS	8.19	<0.0001	8.25	<0.0001
	Vert	11.37	0.001	0.82	NS	1.58	NS
CoD	AP	17.09	<0.0001	0.89	NS	0.63	NS
	ML	23.64	<0.0001	4.47	0.006	4.76	0.004
	Vert	73.54	<0.0001	2.26	NS	3.22	0.028
meanSD	AP	0.50	NS	1.07	NS	1.67	NS
	ML	0.97	NS	1.57	NS	0.60	NS
	Vert	10.89	0.002	10.35	<0.0001	22.19	<0.0001

Results of the two-way mixed-model ANOVA for repeated measures with gait mode and speed as independent factors and the mode–speed interaction. LyE, Lyapunov exponent; CoD, correlation dimension; meanSD, movement variability; AP, anterior–posterior; ML, mediolateral; Vert, vertical; NS, not significant.

Journal of Experimental Biology (2020) 223, jeb224113. doi:10.1242/jeb.224113

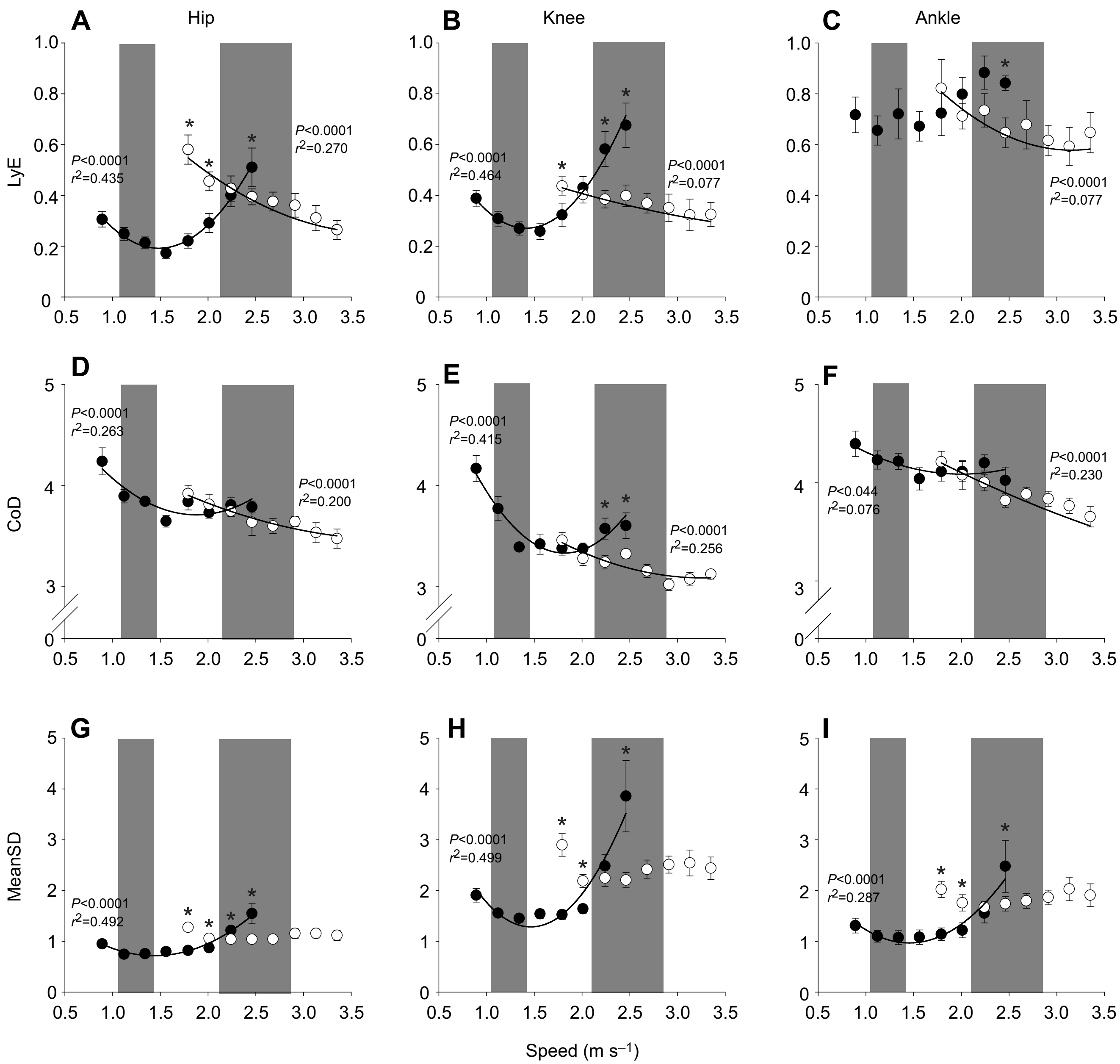

Fig. 2. The largest Lyapunov exponent (LyE), correlation dimension (CoD) and movement variability (meanSD) of the joint angle. Group (n=11) mean±s.e.m. of the LyE (A–C), CoD (D–F) and meanSD (G–I) for the hip, knee and ankle joint angle during walking and running. In the case of a significant effect of speed (mixed-model ANOVA for repeated measures, P<0.005) and a significant curvilinear relationship, a regression line is shown. Gray areas indicate the mean±s.d. of PWS and PRS. *Significant difference in the dependent variable between gait modes (mixed-model ANOVA, P<0.005).

way ANOVA showed a significant gait mode–speed interaction (Table 2) for all three joints. The *post hoc* test revealed that the LyE of the hip joint was significantly higher at the two lowest speeds and significantly lower at the highest speed during running compared with walking (Fig. 2A). For the knee joint, the LyE of running was significantly higher at the lowest speed and lower at the two highest speeds compared with walking (Fig. 2B). For the ankle joint, the LyE during running was significantly lower at the highest speed compared with walking (Fig. 2C).

There was a significant effect of speed on CoD for all three joints during both tasks (Table 1), with significant curvilinear relationships with speed that resembled those of the LyE. The hip and knee joint CoD exhibited U-shaped relationships with speed during walking and decreasing CoD values with increasing speed during running. For the ankle joint, the CoD decreased with speed during both tasks (Fig. 2D–F). There was a significant gait mode–speed interaction for the CoD of the knee joint (Table 2). The *post hoc* test showed that the CoD was significantly higher during walking at the two highest speeds compared with running (Fig. 2E).

There was a significant effect of speed on the meanSD for all three joints during both tasks (Table 1). However, only during walking did the meanSD exhibit a significantly curvilinear relationship with speed (Fig. 2G–I). For all three joints, the meanSD was significantly higher during the highest walking speed compared with the lower speeds. There was a significant gait mode–speed interaction for the meanSD of all three joints (Table 2). For the hip joint, the meanSD was significantly higher during running at the two lowest speeds and significantly lower at the two highest

Journal of Experimental Biology (2020) 223, jeb224113. doi:10.1242/jeb.224113

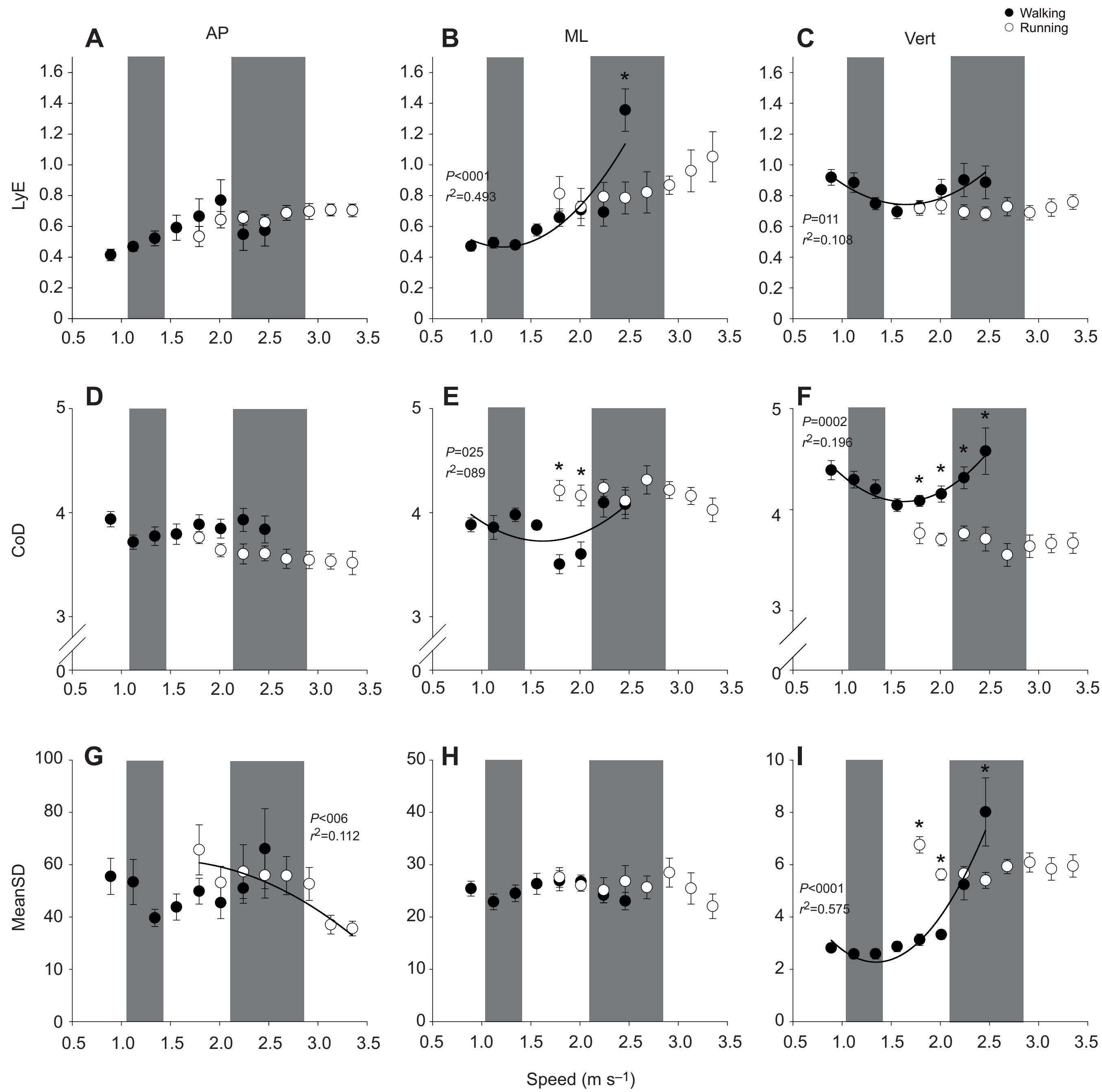

Fig. 3. The largest LyE, CoD and meanSD of the center of mass displacement. Group (*n*=11) mean±s.e.m. of the LyE (A–C), CoD (D–F) and meanSD (G–I) for the center of mass displacement in the anterior–posterior (AP), mediolateral (ML) and vertical (Vert) direction during walking and running. In the case of a significant effect of speed (mixed-model ANOVA for repeated measures, $P<0.005$) and a significant curvilinear relationship, a regression line is shown. Gray areas indicate the mean±s.d. of PWS and PRS. *Significant difference in the dependent variable between gait modes (mixed-model ANOVA, $P<0.005$).

speeds compared with walking (Fig. 2G). For the knee and ankle joint, the meanSD was significantly higher during running at the two lowest speeds and significantly lower at the highest speed compared with walking (Fig. 2H,I).

Center of mass displacements

There was a significant effect of speed on the LyE of the ML and Vert center of mass displacements during walking (Table 1). While the LyE increased curvilinearly with speed in the ML direction, no between-speed differences were observed in the Vert direction (Fig. 3B,C). There was a significant gait mode–speed interaction in the ML direction (Table 2) and the *post hoc* test revealed that the LyE during walking at the highest speed was significantly higher compared with that during running (Fig. 3B).

There was a significant effect of speed on the center of mass CoD in the ML and Vert directions during walking (Table 1). In both cases, a U-shaped relationship was observed, with significantly lower CoD at the intermediate speeds compared with the two highest speeds (Fig. 3E,F). For the ML and Vert directions, there was a significant gait mode–speed interaction (Table 2). In the ML direction, the CoD was significantly higher at the two lowest speeds during running compared with walking (Fig. 3E), and in the Vert

Journal of Experimental Biology

Journal of Experimental Biology (2020) 223, jeb224113. doi:10.1242/jeb.224113

direction, the CoD was significantly higher at all four speeds during walking compared with running (Fig. 3F).

There was a significant effect of speed on the meanSD of the center of mass displacements in the Vert direction during walking and the AP and Vert direction during running (Table 1). In the AP direction during running, the meanSD showed a curvilinear decrease with increasing speed (Fig. 3G), and in the Vert direction, the meanSD increased significantly at the two highest walking speeds (Fig. 3I). There was no significant curvilinear relationship for the Vert center of mass displacement during running. There was a significant gait mode–speed interaction in the Vert direction (Table 2) and the meanSD was significantly higher at the two lowest speeds and higher at the highest speed during running compared with walking (Fig. 3I).

DISCUSSION

The work by Diedrich and Warren (1998, 1995) laid the theoretical foundation for understanding the mechanisms governing the walk-to-run transition in humans from a dynamical systems theory perspective. Based on their studies, two principles can be inferred: the control parameter-dependent attractor stability principle, which suggests that changing locomotion speed above and below the preferred speed of a given gait mode would move the system from a stable attractor to regions of instability, and the attractor stability optimization principle, which suggests the self-selected gait mode at a given speed would exhibit a more stable attractor compared with the alternative non-self-selected gait mode. However, the work by Diedrich and Warren (1998, 1995) was limited by only quantifying the spatial variation in the coordination of segmental motion using relative phase and did not include an assessment of the temporal dynamics of relevant variables. Therefore, the purpose of the present study was to investigate the attractor stability of walking and running across a range of speeds when both stable self-selected movement solutions and unstable non-self-selected movement solutions were evoked. The present study adopted the methodological and analytical approach used by Diedrich and Warren (1995) by quantifying the stability of the executed lower limb coordination pattern using the deviation phase. In addition, the present study quantified the temporal dynamics and movement variability of the lower limb joint angles and the center of mass displacement. In agreement with the inferred principles, it was hypothesized that (1) the movement solution during walking at PWS and during running at PRS is a stable behavioral attractor for that particular gait mode while speeds below and above would display significantly different dynamics and (2) at speeds close to the preferred speed of a particular gait mode, the movement solution would exhibit more stable attractor behavior compared with the alternative gait mode. Additionally, the present study sought to clarify whether a center of mass movement-based or a lower limb joint angle-based attractor behavior constitutes the most appropriate order parameter for human locomotion.

Control parameter-dependent attractor stability principle

The first hypothesis related to the control parameter-dependent attractor stability principle was partially supported. Clear U-shaped relationships with local minima close to the PWS were observed across walking speeds in the mean deviation phase for both the thigh–shank and thigh–foot segment couplings (see Fig. 1C,D), the LyE and CoD for the hip and knee joint angle (see Fig. 2A,B,D,E), and the meanSD for all three joint angles (see Fig. 2G–I). This suggests that the first inferred principle holds true during walking when assessing lower limb coordination stability, when assessing the lower limb temporal dynamics for the hip and knee joint and when assessing movement variability of all three lower limb joints. It is noteworthy that the local minima for the variables in question tended to lie at a speed slightly above the PWS. This specific phenomenon has also been observed in previous studies focusing on the effect of walking speed on the temporal dynamics of lower limb joint angles and stride characteristics (Chien et al., 2015; Jordan et al., 2007; Raffalt et al., 2017). However, it has not been addressed by the previous studies. It could indicate that the PWS is actually an underestimation of the optimal speed for the body and task during walking. This could either be a methodological issue with the PWS assessment, an artifact of altered walking due to the treadmill, or suggest that the PWS is influenced by physiological and psychological aspects unrelated to movement coordination. Interestingly, the results of the present study did not seem to support the application of the control parameter-dependent attractor stability principle to running. For the coordination stability and for the hip and knee joint angle dynamics, there was a clear pattern of increasing attractor stability as running speed increased beyond the preferred running speed; the deviation phase of the thigh–shank segment and thigh–foot segment couplings decreased with increased running speed, as did both the LyE and CoD. This suggests that the factors determining the preferred running speed are not related to the factors determining the attractor stability of running. This apparent difference between walking and running could be explained by the functional role of the lower limb during the two tasks.

During the contact phase of walking, the lower limb functions as an inverted pendulum that moves the center of mass forward across the area of support with a continuous exchange of potential and kinetic energy (Cavagna and Margaria, 1966; Cavagna et al., 1963). Furthermore, during the swing phase, the lower limb functions as double pendulum. Accordingly, the leg swing frequency (i.e. equivalent to the step frequency) at the preferred walking speed equals the resonant frequency of the system, which coincides with a maximal knee joint stability (Russell and Haworth, 2014) and the minimum muscle activity and energy expenditure (Holt et al., 1995; Russell and Apatoczky, 2016). The swinging motion of a pendulum depends on its length, which, in the case of human walking, changes minimally in comparison to overall leg length. This suggests that the self-organization process during walking would seemingly need to adjust for minimal scaling changes in the mechanical properties of the lower limb as compared with more substantial changes in swinging frequency consequential of altered gait speed. Thus, the optimal attractor stability during walking is closely linked to the resonant frequency of the lower limb. In contrast, during the contact phase of running, the lower limb functions as a mechanical spring, in which elastic energy is stored during the initial braking phase and then released during the later propulsion phase (Blickhan, 1989). The efficiency of a spring relates to its stiffness, and it has been shown that leg stiffness is linearly proportional to both running speed and stride frequency (Arampatzis et al., 1999; Farley and González, 1996). The stiffness of the limb is increased by increasing muscle activity surrounding the lower limb joints with the purpose of efficiently utilizing elastic energy (Hobara et al., 2007; Moritani et al., 1991). When analyzing hopping, it has been suggested that as hopping frequency increases, the leg stiffness is increased by greater preactivation of the triceps surae prior to ground contact. This occurs in conjunction with an altered short-latency stretch reflex response (Hobara et al., 2007; Voigt et al., 1998). Similar changes in reflex and EMG responses have been observed during running with increasing speeds (Simonsen et al., 2012), when the stride

Journal of Experimental Biology

frequency increases and contact time decreases simultaneously. This would suggest that the control mechanism for increasing the leg stiffness simplifies, making the entire spring system simpler with fewer degrees of freedom. Simplifying one or more components in the self-organization process may permit greater attractor stability. Furthermore, during running, the forward swinging motion of the leg requires a higher angular velocity than can be created alone by the pendulum motion caused by gravity. Therefore, considerable muscle activity in hip flexor muscles is required to generate the needed torque (Modica and Kram, 2005). Thus, because of this speed-related change in mechanical properties and control mechanisms of the spring components and the added torque to the pendulum motion, it may be unfeasible to reach an optimum in attractor stability during running at the speeds used in the present study.

It is noteworthy that the highest running speed of the present study was 3.35 m s^{-1} (equal to 12.1 km h^{-1} or 7.5 mph). This is well below what many healthy individuals are capable of running at and it is possible that the attractor stability would eventually decrease if higher running speeds were tested. If that was the case, it would provide evidence to confirm the control parameter-dependent attractor stability principle for running as well. However, for safety reasons, testing this would have required more experienced treadmill runners. Furthermore, running and sprinting at very high speeds will alter the foot strike pattern for most individuals from a heel strike pattern to a forefoot strike pattern. It is possible that a change in foot strike pattern with increasing speed would affect the self-organization process of the system and significantly change the attractor stability. However, it is beyond the scope of this study to elucidate this aspect.

Attractor stability optimization principle

The second hypothesis related to the attractor stability optimization principle stated that the movement solution would exhibit more stable attractor behavior at speeds close to the preferred speed of that particular gait mode compared with the alternative gait mode. A more stable attractor behavior would be characterized by a low deviation phase when using the relative phase approach, by a coinciding low LyE and CoD when assessing the dynamics of the attractor behavior, and by a low meanSD when assessing movement variability. This hypothesis was supported for the relative phase approach, for the dynamics of the attractor behavior of the hip and knee joint angles, and for the movement variability of all three joints but not for the center of mass displacement. First, a lower deviation phase for both joint couplings (see Fig. 1C,D), and a lower LyE and lower movement variability for the hip and knee joint angles (see Fig. 2A,B,G,H) were observed during walking compared with running at 1.79 m s^{-1}. Second, at 2.46 m s^{-1}, running elicited a lower deviation phase for both joint couplings, a lower LyE and lower movement variability for the hip and knee joint angles compared with walking.

The results for attractor stability when assessed with deviation phase verify the results presented by Diedrich and Warren (1995), and show that the attractor stability was highest at a particular gait mode at speeds closest to the corresponding mode's preferred speed. This was true for both the thigh–shank segment and the thigh–foot segment couplings. While this supports the attractor stability optimization principle, the applied methodology does not take into account the temporal dynamics of the system. Thus, it is crucial to also evaluate the principle in question through an assessment of the temporal dynamics of the attractor behavior. This was achieved in the present study by quantifying the LyE and CoD of the hip, knee and ankle joint angles and the center of mass displacement. It was evident that the principle also holds true for the dynamics of the hip and knee joint angles and to a lesser extent for the ankle joint angle. This phenomenon was not observed for the center of mass displacements. Our results clearly demonstrate that for the hip and knee joint dynamics, the self-selected gait mode at a given speed was characterized by a more stable attractor compared with that of the alternative non-self-selected gait mode. In relation to the functional role of the lower limb and the self-organization process, this indicates that forcing the leg to function as a spring (i.e. running) is inexpedient when the constraints of the tasks (relatively low speed) favor an inverted pendulum function (i.e. walking) to create a stable attractor behavior. Equally, forcing an inverted pendulum function when the task constraints favor a spring function seems inexpedient at relatively high speeds. The results of the present study suggest that the hip and knee joint angles and the corresponding oscillatory motion of the thigh and shank segment are better for determining the limb function than the ankle joint and foot segment motion. When quantifying the attractor stability through the movement variability of the joint angles, the principle was also confirmed. Thus, the movement variability was observed to be lower at a given speed when using the self-selected gait mode. However, assessing movement variability via meanSD suffers from the same limitation as the relative phase approach by not incorporating the temporal dynamics, which is a key element of any non-linear dynamical system (Stergiou, 2004, 2016).

The walk-to-run transition speed and the run-to-walk transition speed (neither measured in the present study) are expected to lie somewhere between the PWS and the PRS. In the present study, both walking and running were performed at four different speeds between the PWS and PRS. The attractor stability for one gait mode increased beyond the stability for the alternative mode within these four speeds, indicating that the gait mode transition lies between these four speeds. Furthermore, for one or both of the two intermediate speeds (2.01 and 2.24 m s^{-1}), the attractor stability was nearly the same, suggesting that neither of the two gait modes outperformed the other. However, when the speed was either decreased or increased slightly to either 1.79 or 2.46, a clear favorable movement solution was available. In support of the notion presented by Diedrich and Warren (1995), the present study suggests that the choice to walk or run at a given speed is determined by whatever gait mode provides the highest lower limb attractor stability.

Human locomotion order parameter

The present study had a secondary purpose of identifying an appropriate order parameter for walking and running. No clear consensus exists in the literature and various variables related to the center of mass or the lower limb motions have been used (Diedrich and Warren, 1995; Dingwell and Marin, 2006; England and Granata, 2007; Kurz et al., 2005; Raffalt et al., 2017; Stergiou et al., 2001). In the present study, it was speculated that the variable(s) supporting the raised hypotheses would be the most appropriate order parameter(s) for capturing the system dynamics during locomotion. Our results suggest that variables that incorporated the lower limb motions are superior in describing the attractor behavior of the system, compared with variables based on the center of mass displacement. In particular, the deviation phase, which describes the stability of the oscillatory segment coupling, and the LyE and CoD, which describe the temporal dynamics of the hip and knee joint angles, seemed to clearly capture the changes in attractor behavior as speed was increased or movement task was changed.

Journal of Experimental Biology

Notably, the temporal dynamics and the movement variability of the center of mass displacements did not support the two inferred principles, and no consistent pattern could be observed across the three directions as speed or movement task was changed (see Fig. 3). These observations question the use of center of mass movements when evaluating the system's attractor behavior during locomotion. Previously, quantifying LyE of center of mass movements has been linked to the overall stability of gait and the risk of falling (Bruijn et al., 2012, 2013). However, very different results have been reported in the literature when assessing LyE on the center of mass movements during walking at different speeds (Bruijn et al., 2009; Dingwell and Marin, 2006; Raffalt et al., 2017). While this potentially may be due to different methodological approaches (Raffalt et al., 2019; Stenum et al., 2014), based on the results of the present study, caution should be exercised when using the center of mass motion as an order parameter for human locomotion.

While not appropriate as an order parameter for human locomotion when addressing attractor behavior, the vertical center of mass displacement in particular seems closely related to the energetics of walking (Gottschall and Kram, 2003; Grabowski, 2010; Wurdeman et al., 2017). Thus, the dynamics and movement variability of the vertical center of mass displacement in the present study best resembled the U-shaped relationship between oxygen uptake and walking speed previously observed (Raffalt et al., 2017; Ralston, 1958; Zarrugh et al., 1974).

Study limitation

The present study used absolute speeds similar to the study by Bruijn et al. (2009). This is in contrast to studies that have used either Froude number-based speeds (Diedrich and Warren, 1998, 1995; England and Granata, 2007; Raffalt et al., 2017) or relative PWS (Chien et al., 2015; Dingwell and Marin, 2006). There are pros and cons for each approach; however, when designing this protocol, we prioritized the inclusion of four speeds at which all participants were able to both walk and run.

The method of identifying PWS and PRS was adopted from Dingwell and Marin (2006), who used it only to find PWS. While there is no reason to believe that the method is inappropriate for running, it is possible that the method is less effective when applied to running. This may further explain differences in the observations for running compared with walking in the present study. The PRS observed in the present study was relatively low compared with preferred speeds that might be expected in competitive runners. Thus, the results of the present study cannot be extrapolated to individuals with substantial running experience.

Conclusion

In conclusion, the present study showed that lower limb attractor stability during walking is maximized at speeds close to PWS. For running, however, lower limb attractor stability increases as running speed is increased beyond PRS. Furthermore, the present study showed that the attractor stability is highest at a particular gait mode closest to the corresponding preferred speed. These results provide confirmation of the observations made by Diedrich and Warren (1998, 1995) and support the control parameter-dependent attractor stability principle and the attractor stability optimization principle inferred from their studies. Finally, the present study suggests that the dynamics and relative phase of lower limb motion provide a more appropriate order parameter for quantifying attractor behavior during human locomotion compared with the dynamics of center of mass displacement.

Acknowledgements
The authors thank Chase Rock for his assistance in data collection, and Ernst Albin Hansen, Aalborg University, for fruitful feedback on the manuscript.

Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: J.A.K., S.R.W., N.S.; Methodology: P.C.R., J.A.K., S.R.W., N.S.; Formal analysis: P.C.R.; Investigation: P.C.R., J.A.K., S.R.W.; Writing - original draft: P.C.R., J.A.K., S.R.W., N.S.; Writing - review & editing: P.C.R., J.A.K., S.R.W., N.S.; Funding acquisition: S.R.W., N.S.

Funding
This work was supported by the Center for Research in Human Movement Variability and the National Institutes of Health (P20GM109090 and R15HD08682). Deposited in PMC for release after 12 months.

References

Alexander, R. M. (1977). Mechanics and scaling of terrestial locomotion. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 93-110. New York, US: Academic Press.

Arampatzis, A., Brüggemann, G.-P. and Metzler, V. (1999). The effect of speed on leg stiffness and joint kinetics in human running. *J. Biomech.* **32**, 1349-1353. doi:10.1016/S0021-9290(99)00133-5

Biewener, A. A. and Taylor, C. R. (1986). Bone strain: a determinant of gait and speed? *J. Exp. Biol.* **123**, 383-400.

Biewener, A. A., Thomason, J., Goodship, A. and Lanyon, L. E. (1983). Bone stress in the horse forelimb during locomotion at different gaits: a comparison of two experimental methods. *J. Biomech.* **16**, 565-576. doi:10.1016/0021-9290(83)90107-0

Blickhan, R. (1989). The spring-mass model for running and hopping. *J. Biomech.* **22**, 1217-1227. doi:10.1016/0021-9290(89)90224-8

Bruijn, S. M., van Dieën, J. H., Meijer, O. G. and Beek, P. J. (2009). Is slow walking more stable? *J. Biomech.* **42**, 1506-1512. doi:10.1016/j.jbiomech.2009.03.047

Bruijn, S. M., Bregman, D. J. J., Meijer, O. G., Beek, P. J. and van Dieën, J. H. (2012). Maximum Lyapunov exponents as predictors of global gait stability: a modelling approach. *Med. Eng. Phys.* **34**, 428-436. doi:10.1016/j.medengphy.2011.07.024

Bruijn, S. M., Meijer, O. G., Beek, P. J. and van Dieën, J. H. (2013). Assessing the stability of human locomotion: a review of current measures. *J. R. Soc. Interface* **10**, 20120999. doi:10.1098/rsif.2012.0999

Caggiano, V., Leiras, R., Goñi-Erro, H., Masini, D., Bellardita, C., Bouvier, J., Caldeira, V., Fisone, G. and Kiehn, O. (2018). Midbrain circuits that set locomotor speed and gait selection. *Nature* **553**, 455-460. doi:10.1038/nature25448

Cavagna, G. A. and Margaria, R. (1966). Mechanics of walking. *J. Appl. Physiol.* **21**, 271-278. doi:10.1152/jappl.1966.21.1.271

Cavagna, G. A., Saibene, F. P. and Margaria, R. (1963). External work in walking. *J. Appl. Physiol.* **18**, 1-9. doi:10.1152/jappl.1963.18.1.1

Chien, J. H., Yentes, J., Stergiou, N. and Siu, K. C. (2015). The effect of walking speed on gait variability in healthy young, middle-aged and elderly individuals. *J. Phys. Act. Nutr. Rehabil.* **2015**.

Diedrich, F. J. and Warren, W. H., Jr. (1995). Why change gaits? Dynamics of the walk-run transition. *J. Exp. Psychol. Hum. Percept. Perform.* **21**, 183-202. doi:10.1037/0096-1523.21.1.183

Diedrich, F. J. and Warren, W. H. (1998). The dynamics of gait transitions: effects of grade and load. *J. Mot. Behav.* **30**, 60-78. doi:10.1080/00222899809601323

Dingwell, J. B. and Marin, L. C. (2006). Kinematic variability and local dynamic stability of upper body motions when walking at different speeds. *J. Biomech.* **39**, 444-452. doi:10.1016/j.jbiomech.2004.12.014

England, S. A. and Granata, K. P. (2007). The influence of gait speed on local dynamic stability of walking. *Gait Posture* **25**, 172-178. doi:10.1016/j.gaitpost.2006.03.003

Farley, C. T. and González, O. (1996). Leg stiffness and stride frequency in human running. *J. Biomech.* **29**, 181-186. doi:10.1016/0021-9290(95)00029-1

Farley, C. T. and Taylor, C. R. (1991). A mechanical trigger for the trot-gallop transition in horses. *Science* **253**, 306-308. doi:10.1126/science.1857965

Gottschall, J. S. and Kram, R. (2003). Energy cost and muscular activity required for propulsion during walking. *J. Appl. Physiol.* **94**, 1766-1772. doi:10.1152/japplphysiol.00670.2002

Grabowski, A. M. (2010). Metabolic and biomechanical effects of velocity and weight support using a lower-body positive pressure device during walking. *Arch. Phys. Med. Rehabil.* **91**, 951-957. doi:10.1016/j.apmr.2010.02.007

Grassberger, P. and Procaccia, I. (1983). Measuring the strangeness of strange attractors. *Physica D* **9**, 189-208. doi:10.1016/0167-2789(83)90298-1

Haken, H. (1983). *Synergetics, An Introduction*. Berlin, Germany: Springer.

Haken, H., Kelso, J. A. S. and Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biol. Cybern.* **51**, 347-356. doi:10.1007/BF00336922

Hamill, J., van Emmerik, R. E. A., Heiderscheit, B. C. and Li, L. (1999). A dynamical systems approach to lower extremity running injuries. *Clin. Biomech.* **14**, 297-308. doi:10.1016/S0268-0033(98)90092-4

Hansen, E. A., Kristensen, L. A. R., Nielsen, A. M., Voigt, M. and Madeleine, P. (2017). The role of stride frequency for walk-to-run transition in humans. *Sci. Rep.* **7**, 2010. doi:10.1038/s41598-017-01972-1

Hobara, H., Kanosue, K. and Suzuki, S. (2007). Changes in muscle activity with increase in leg stiffness during hopping. *Neurosci. Lett.* **418**, 55-59. doi:10.1016/j.neulet.2007.02.064

Holt, K. G., Jeng, S. F., Ratcliffe, R. and Hamill, J. (1995). Energetic cost and stability during human walking at the preferred stride frequency. *J. Mot. Behav.* **27**, 164-178. doi:10.1080/00222895.1995.9941708

Hoyt, D. F. and Taylor, C. R. (1981). Gait and the energetics of locomotion in horses. *Nature* **292**, 239. doi:10.1038/292239a0

Hreljac, A. (1993a). Determinants of the gait transition speed during human locomotion: kinetic factors. *Gait Posture* **1**, 217-223. doi:10.1016/0966-6362(93)90049-7

Hreljac, A. (1993b). Preferred and energetically optimal gait transition speeds in human locomotion. *Med. Sci. Sports Exerc.* **25**, 1158-1162. doi:10.1249/00005768-199310000-00012

Hreljac, A. (1995a). Determinants of the gait transition speed during human locomotion: kinematic factors. *J. Biomech.* **28**, 669-677. doi:10.1016/0021-9290(94)00120-S

Hreljac, A. (1995b). Effects of physical characteristics on the gait transition speed during human locomotion. *Hum. Mov. Sci.* **14**, 205-216. doi:10.1016/0167-9457(95)00017-M

James, C. R. (2004). Considerations of movement variability in biomechanics research. In *Innovative Analyses of Human Movement - Analytical Tools for Human Movement Research* (ed. N. Stergiou), pp. 29-62. Champaign, IL, USA: Human Kinetics.

Jordan, K., Challis, J. H. and Newell, K. M. (2006). Long range correlations in the stride interval of running. *Gait Posture* **24**, 120-125. doi:10.1016/j.gaitpost.2005.08.003

Jordan, K., Challis, J. H. and Newell, K. M. (2007). Walking speed influences on gait cycle variability. *Gait Posture* **26**, 128-134. doi:10.1016/j.gaitpost.2006.08.010

Kelso, J. A. S. and Schöner, G. (1988). Self-organization of coordinative movement patterns. *Hum. Mov. Sci.* **7**, 27-46. doi:10.1016/0167-9457(88)90003-6

Kelso, J. A., Southard, D. L. and Goodman, D. (1979). On the nature of human interlimb coordination. *Science* **203**, 1029-1031. doi:10.1126/science.424729

Kiehn, O. (2016). Decoding the organization of spinal circuits that control locomotion. *Nat. Rev. Neurosci.* **17**, 224-238. doi:10.1038/nrn.2016.9

Kram, R., Domingo, A. and Ferris, D. P. (1997). Effect of reduced gravity on the preferred walk-run transition speed. *J. Exp. Biol.* **200**, 821-826.

Kurz, M. J. and Stergiou, N. (2004). Applied dynamic systems theory for the analysis of movement. In *Innovative Analyses of Human Movement. Analytical Tools for Human Movement Research* (ed. N. Stergiou), pp. 93-119. Champaign, IL: Human Kinetics.

Kurz, M. J., Stergiou, N., Buzzi, U. H. and Georgoulis, A. D. (2005). The effect of anterior cruciate ligament reconstruction on lower extremity relative phase dynamics during walking and running. *Knee Surg. Sports Traumatol. Arthrosc.* **13**, 107-115. doi:10.1007/s00167-004-0554-0

Lamoth, C. J. C., Beek, P. J. and Meijer, O. G. (2002). Pelvis-thorax coordination in the transverse plane during gait. *Gait Posture* **16**, 101-114. doi:10.1016/S0966-6362(01)00146-1

Minetti, A. E., Ardigo, L. P. and Saibene, F. (1994). The transition between walking and running in humans: metabolic and mechanical aspects at different gradients. *Acta Physiol. Scand.* **150**, 315-323. doi:10.1111/j.1748-1716.1994.tb09692.x

Modica, J. R. and Kram, R. (2005). Metabolic energy and muscular activity required for leg swing in running. *J. Appl. Physiol.* **98**, 2126-2131. doi:10.1152/japplphysiol.00511.2004

Moritani, T., Oddsson, L. and Thorstensson, A. (1991). Phase-dependent preferential activation of the soleus and gastrocnemius muscles during hopping in humans. *J. Electromyogr. Kinesiol.* **1**, 34-40. doi:10.1016/1050-6411(91)90024-Y

Newell, K. M. and Corcos, D. M. (1993). *Variability and Motor Control*: Human Kinetics Publishers.

Prilutsky, B. I. and Gregor, R. J. (2001). Swing- and support-related muscle actions differentially trigger human walk-run and run-walk transitions. *J. Exp. Biol.* **204**, 2277-2287.

Raffalt, P. C., Guul, M. K., Nielsen, A. N., Puthusserypady, S. and Alkjær, T. (2017). Economy, movement dynamics, and muscle activity of human walking at different speeds. *Sci. Rep.* **7**, 43986. doi:10.1038/srep43986

Raffalt, P. C., Kent, J. A., Wurdeman, S. R. and Stergiou, N. (2019). Selection procedures for the largest lyapunov exponent in gait biomechanics. *Ann. Biomed. Eng.* **47**, 913-923. doi:10.1007/s10439-019-02216-1

Ralston, H. J. (1958). Energy-speed relation and optimal speed during level walking. *Int. Z. Angew. Physiol.* **17**, 277-283. doi:10.1007/BF00698754

Ranisavljev, I., Ilic, V., Markovic, S., Soldatovic, I., Stefanovic, D. and Jaric, S. (2014). The relationship between hip, knee and ankle muscle mechanical characteristics and gait transition speed. *Hum. Mov. Sci.* **38**, 47-57. doi:10.1016/j.humov.2014.08.006

Russell, D. M. and Apatoczky, D. T. (2016). Walking at the preferred stride frequency minimizes muscle activity. *Gait Posture* **45**, 181-186. doi:10.1016/j.gaitpost.2016.01.027

Russell, D. M. and Haworth, J. L. (2014). Walking at the preferred stride frequency maximizes local dynamic stability of knee motion. *J. Biomech.* **47**, 102-108. doi:10.1016/j.jbiomech.2013.10.012

Sauer, T. and Yorke, J. A. (1993). How many delay coordinates do you need? *Int. J. Bifurc. Chaos* **3**, 737-744. doi:10.1142/S0218127493000647

Sauer, T., Yorke, J. A. and Casdagli, M. (1991). Embedology. *J. Stat. Phys.* **65**, 579-616. doi:10.1007/BF01053745

Simonsen, E. B., Alkjær, T. and Raffalt, P. C. (2012). Reflex response and control of the human soleus and gastrocnemius muscles during walking and running at increasing velocity. *Exp. Brain Res.* **219**, 163-174. doi:10.1007/s00221-012-3075-y

Stenum, J., Bruijn, S. M. and Jensen, B. R. (2014). The effect of walking speed on local dynamic stability is sensitive to calculation methods. *J. Biomech.* **47**, 3776-3779. doi:10.1016/j.jbiomech.2014.09.020

Stergiou, N. (2004). *Innovative Analyses of Human Movement*. Champaign, Illinois, USA: Human Kinetics.

Stergiou, N. (2016). *Nonlinear Analysis for Human Movement Variability*. Boca Raton, Florida, USA: Taylor & Francis Group.

Stergiou, N., Jensen, J. L., Bates, B. T., Scholten, S. D. and Tzetzis, G. (2001). A dynamical systems investigation of lower extremity coordination during running over obstacles. *Clin. Biomech.* **16**, 213-221. doi:10.1016/S0268-0033(00)00090-5

Takens, F. (1981). Detecting strange attractors in turbulence. *Dyn. Syst. Turbulence Lecture Notes in Mathematics* **898**, 366-381. doi:10.1007/BFb0091924

Taylor, C. R. (1985). Force development during sustained locomotion: a determinant of gait, speed and metabolic power. *J. Exp. Biol.* **115**, 253-262.

Thorstensson, A. and Roberthson, H. (1987). Adaptations to changing speed in human locomotion: speed of transition between walking and running. *Acta Physiol. Scand.* **131**, 211-214. doi:10.1111/j.1748-1716.1987.tb08228.x

Vaughan, C. L., Davis, B. L. and O'Conner, J. C. (1992). *Dynamics of Human Gait*. Champaign, IL: Human Kinetics.

Voigt, M., Dyhre-Poulsen, P. and Simonsen, E. B. (1998). Modulation of short latency stretch reflexes during human hopping. *Acta Physiol. Scand.* **163**, 181-194. doi:10.1046/j.1365-201X.1998.00351.x

Voigt, M., Hyttel, M. K., Jakobsen, L. S., Jensen, M. K., Balle, H. and Hansen, E. A. (2019). Human walk-to-run transition in the context of the behaviour of complex systems. *Hum. Mov. Sci.* **67**, 102509-102509. doi:10.1016/j.humov.2019.102509

Wolf, A., Swift, J. B., Swinney, H. L. and Vastano, J. A. (1985). Determining lyapunov exponents from a time series. *Physica D* **16**, 285-317. doi:10.1016/0167-2789(85)90011-9

Wurdeman, S. R. (2016). State-space reconstruction. In *Nonlinear Analysis for Human Movement Variability* (ed. N. Stergiou), pp. 55-82. Boca Raton, FL, USA: CRC Press.

Wurdeman, S. R., Raffalt, P. C. and Stergiou, N. (2017). Reduced vertical displacement of the center of mass is not accompanied by reduced oxygen uptake during walking. *Sci. Rep.* **7**, 17182. doi:10.1038/s41598-017-17532-6

Zarrugh, M. Y., Todd, F. N. and Ralston, H. J. (1974). Optimization of energy expenditure during level walking. *Eur. J. Appl. Physiol. Occup. Physiol.* **33**, 293-306. doi:10.1007/BF00430237