Kinematics of walking and running in ostriches (Struthio camelus): insights into the walk-run transition

J. Rubenson¹, T. Farrell¹, D. Heliams², S.K. Maloney³, P.C. Withers⁴, G.B.M. Martin⁵, D.G. Lloyd¹, P.A. Fournier¹

¹Department of Human Movement and Exercise Science, UWA, Nedlands/Australia
²Fauna Technologies, Perth/Australia
³Department of Physiology, UWA, Nedlands/Australia
⁴Department of Zoology, UWA, Nedlands/Australia
⁵Animal Science Group, Department of Agriculture, UWA, Nedlands/Australia

Introduction

In order to accommodate an increase in speed, humans and other terrestrial animals change from a walk to a run (or trot, or hop, as is the case in quadrupedal and saltatorial locomotion respectively). Walking is defined as a gait where at least one foot is in contact with the ground at all times¹². Walking is also characterised in terms of an ‘inverted pendulum’, where the gravitational-potential and kinetic energies of the body’s center of mass are out-of-phase³. Unlike walking, running is defined by an aerial phase, where no feet are in contact with the ground¹² and is characterised in terms of a ‘bouncing ball’, where the gravitational-potential and kinetic energies of the center of mass are in-phase³.

Although extensive research has been directed to understanding the underlying cause of the walk-run transition, there is still no clear answer to this question. From work done on humans⁴ and horses⁵, it has become a popular view that the metabolic cost of locomotion triggers the walk-run transition. These studies indicate that, at speeds above the walk-run, and walk-trot transitions, walking becomes metabolically more expensive, and hence less beneficial.

Humans are the only bipedal species for which both metabolic, and mechanical, triggers of the walk-run transition have been examined. What is not clear is whether the causes of the walk–run transition is common to all bipedal runners. An investigation into the mechanics and energetics of gait transition in avian bipedal runners is an approach of choice for explaining how general are the principles governing gait transition, and may help to resolve the determinants of the walk-run transition in humans. To this extent we explored whether the transition from walking to running in ostriches (the bipedal species closest in mass to adult humans) exhibited any clear metabolic and/or mechanical triggers.

Methods

Two male and two female ostriches (average mass 66.1 ± 6.09 kg; mean ± S.D.) were trained to run on a motorised treadmill over a 6 month period. The birds’ rates of oxygen consumption were measured at rest and at speeds ranging from 1.0 to 4.0 m/s using an open-flow metabolic system⁶⁷. Oxygen consumption was converted to energy cost of transport (J/kg/m) using an energy equivalent of 20.1 J ml⁻¹O₂ and dividing by walking/running velocity. The birds were videod in lateral view (PEAK motion analysis system, 200Hz). Joint centers were identified from marker sets placed on the pelvis, tibiotarsus and tarsometatarsus in conjunction with an anatomical model of the ostrich’s lower limb. The captured video was analysed using PEAK motion analysis system software.

Results & Discussion

In this study we were unable to train our ostriches to walk at speeds above their preferred walk-run transition speed, or to run at speeds below it. However, if changing from a walk to a run is strongly coupled to metabolic energetics, a breakpoint favoring a lower cost of locomotion may still be detectable when an animal adopts its preferred gait transition speed (this is evident from data on humans and horses).
Our results did not show a breakpoint in the energy cost of locomotion when the ostriches began to run (Fig. 1). Nevertheless, at the walking speed of 2 m/s a break in the linear increase in metabolic cost of transport with speed was indeed observed (Fig. 1). From our kinematic analysis it was also found that, above 2 m/s, the ostriches ceased to behave as an inverted pendulum, where the gravitational-potential and kinetic energies of the body’s center of mass are out of phase, and instead, exhibited a bouncing-like walk, where the gravitational-potential and kinetic energies of the center of mass are in-phase.

Figure 1: The net metabolic cost of transport as a function of speed in ostriches. Walking and running speeds are indicated by the arrows at the bottom of the graph and the walk-run transition by the dashed line. $E_p$ and $E_{kh}$ refer to the gravitational-potential energy and horizontal kinetic energy of the body’s center of mass respectively.

Our results indicate both important similarities and differences between the characteristics of gait transition in humans and ostriches. In contrast to humans, ostriches; 1) exhibit no sharp kinematic transitions (e.g. duty factor) at the walk-run transition; 2) do not show a breakpoint in the relationship between energy cost of transport and speed at the walk-run transition; and 3) undergo a transition from a pendulum-like gait to a bouncing-like gait without an accompanying aerial phase. However, similar to humans, when ostriches switch from a pendulum-like gait to a bouncing-like gait, a breakpoint favoring a lower energy cost of transport is observed.

These findings provide insights into the general principles governing gait transition in bipeds, as well as the specific nature of gait transition in humans. We have demonstrated that the transition from a gait where one foot is always in contact with the ground, to one where an aerial phase is present, (i.e. walking to running) is not necessarily governed by metabolic energetics. In agreement with others, we have also demonstrated that the transition from a pendulum-like gait to a bouncing-like gait saves metabolic energy, but have, for the first time, demonstrated that this can occur in absence of an aerial phase. This raises an important question: why the transition to an energy-saving, bouncing-like gait, is associated with an aerial phase in humans but not in ostriches? Answering this question will prove important for understanding the underlying mechanisms behind the walk-run transition in humans and bipeds in general.
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