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Grounded running in quails: Simulations indicate benefits of observed fixed aperture angle between legs before touch-down

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HIGHLIGHTS

- With experiments and simulations we investigated grounded running.
- Quails fixed the angle between legs (aperture angle) before touch-down.
- Aperture angle correlates with dynamical relevant parameters.
- Fixed angle of attack strategy is not feasible for grounded running.
- The fixed aperture angle strategy improved model stability.

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ABSTRACT

Many birds use grounded running (running without aerial phases) in a wide range of speeds. Contrary to walking and running, numerical investigations of this gait based on the BSLIP (bipedal spring loaded inverted pendulum) template are rare. To obtain template related parameters of quails (e.g. leg stiffness) we used x-ray cinematography combined with ground reaction force measurements of quail grounded running. Interestingly, with speed the quails did not adjust the swing leg's angle of attack with respect to the ground but adapted the angle between legs (which we termed aperture angle), and fixed it about 30 ms before touchdown. In simulations with the BSLIP we compared this swing leg alignment policy with the fixed angle of attack with respect to the ground typically used in the literature. We found symmetric periodic grounded running in a simply connected subset comprising one third of the investigated parameter space. The fixed aperture angle strategy revealed improved local stability and surprising tolerance with respect to large perturbations. Starting with the periodic solutions, after step-down step-up or step-up step-down perturbations of 10% leg rest length, in the vast majority of cases the bipedal SLIP could accomplish at least 50 steps to fall. The fixed angle of attack strategy was not feasible. We propose that, in small animals in particular, grounded running may be a common gait that allows highly compliant systems to exploit energy storage without the necessity of quick changes in the locomotor program when facing perturbations.

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1. Introduction

Gait categories, based on duty factor, do not necessarily correspond to functional categories based on overall leg behaviour or center of mass (CoM) movement (i.e. pendulum-like or spring-like behavior (Cavagna et al., 1976)). In avian terrestrial locomotion, three gaits are frequently observed: walking, grounded running (Hancock et al., 2007; Nudds et al., 2011; Rubenson et al., 2004) (also referred to as compliant walking (Clark and Alexander, 1975)), and running (also referred to as

aerial running (Nudds et al., 2011)). Grounded running combines duty factors traditionally linked to walking (duty factors > 0.5, i.e. double support phases exist) with running-like energy fluctuations of the body, i.e. potential and kinetic energy change nearly in phase (Cavagna 1975; Heglund et al., 1982). While the evolutionary relevance of both walking and running and some of the optimization criteria and constraints imposed by these gaits on the locomotor system are well documented for birds and humans (Hancock et al., 2007; Nudds et al., 2011; Rubenson et al., 2004; Clark and Alexander, 1975; Heglund et al., 1982; Saibene and Minetti, 2003; Minetti et al., 1994; Gatesy and Biewener, 1991; Gatesy and Middleton, 1997; Muir et al., 1996), they are not as clear for grounded running.

For activities such as exploration and foraging birds favor the walking gait. Running allows them to escape from predators, or to

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Nomenclature

CoM	body center of mass
CoP	center of pressure
GRF	ground reaction force
BW	body weight
SSPh	single support phase
DSPH	double support phase
mp	maximum protraction
tob	tip of beak
occ	occiput
cmc	caudalmost cervical vertebrae
tomt	tip of middle toe
TD	touch down
TO	take off
a, v, s	acceleration, speed and position of the CoM
SLIP	spring loaded inverted pendulum
LTP	lower turning point
α_{leg}	leg orientation
α	virtual leg orientation
α_0	angle of attack at touch-down

ϕ_{leg}	aperture angle between legs
ϕ_{leg0}	aperture angle between legs at touch-down
$\phi;$	aperture angle between virtual legs
ϕ_0	aperture angle between virtual legs at touch-down
m	body mass
k	spring stiffness
g	gravity
l_0	spring rest length
E	system energy
E_p	potential energy
E_k	kinetic energy
ω_0	natural frequency of the system
\hat{k}	dimensionless leg stiffness
\hat{l}_0	dimensionless rest length
\hat{x}_{rel}, \hat{y}	system state variables
\hat{E}	dimensionless system energy
ψ	leg compression
GR	grounded running speed
P	Poincaré map
DP	linearized Poincaré map
λ_i	eigenvalues of the linearized Poincaré map

travel long distances economically at higher speeds (Hancock et al., 2007; Nudds et al., 2011; Rubenson et al., 2004; Heglund et al., 1982). It has been hypothesized that grounded running associated with more compliant limbs may facilitate the control of head movements, thereby improving visual stability (Hancock et al., 2007). Transitioning between walking and grounded running has also been associated with a reduction in the metabolic cost of transport in the ostrich (Rubenson et al., 2004). Others have suggested that always keeping at least one foot in contact with the ground provides the ability to perform fast turns, something which in the wild may be more relevant than energy saving or speed (Gatesy and Biewener, 1991; Daley and Usherwood, 2010).

Apart from economic considerations, simulations of walking and running using the bipedal spring-loaded inverted pendulum model (BSLIP) indicate the exploitation of self-stable modes in bipedal locomotion (Seyfarth et al., 2002, 2003; Geyer et al., 2006). Although animals use numerous sensory and neuromuscular mechanisms during movement (e.g. Pearson, 1995; Dietz, 1996), the use of self-stable modes, i.e. tuning parameters like leg stiffness to regions of BSLIP stability, may relax the required neural control in coping with internal or external perturbations during locomotion (Blickhan et al., 2007). For example, BSLIP parameters adopted by humans in running and walking mostly correspond to BSLIP regions of stability (Seyfarth et al., 2002, 2003; Geyer et al., 2006).

Contrary to walking and running (e.g. Seyfarth et al., 2002, 2003; Geyer et al., 2006; Blickhan, 1989), numerical investigations on grounded running are rare. Recently Rummel et al. (2009) reported periodic BSLIP grounded running within a very narrow range of rather slow speeds, steep contact angles and constant high stiffness. It is however not known whether periodic grounded running can be generated by the BSLIP model in the parameter space that birds prefer. Moreover, it is not clear how simple swing leg control strategies might influence the stability of such eventual periodic solutions.

In preliminary experiments we observed that, during grounded running, the angle between legs (which we termed aperture angle) was fixed by the quails in a time period before touchdown. This fixed aperture angle between legs represents a swing leg retraction scheme not reported before. It leads to swing leg retraction related to stance leg rotation. In contrast, in BSLIP

simulations of locomotion the swing leg is typically held at a constant angle with respect to the ground (Seyfarth et al., 2002, 2003; Geyer et al., 2006).

In this paper, we experimentally verify the use of a fixed aperture angle in quail grounded running and numerically analyze possible benefits of this leg alignment strategy compared to the fixed angle of attack. To this end, we estimate BSLIP related dimensionless parameters (e.g. leg stiffness, leg length, angle of attack, aperture angle) using kinematic x-ray motion analysis and single limb force plate measurements during quail grounded running. Within the obtained parameter range we analyze the stability of grounded BSLIP running applying both leg alignment strategies. Finally, we compare and discuss model predictions with experimental findings.

2. Methods

2.1. Experiments

For our investigation of steady grounded running we disregarded trials with (1) the CoP of any leg being outside the force plate area (2) a horizontal speed deviation of more than 5% between the force plates (non-steady state trials); (3) aerial phases; and (4) a phase shift between potential (E_p) and kinetic energy (E_k) above 45° (non-bouncing mechanics) (Ahn et al., 2004). We obtained E_p and E_k as described by Cavagna (1975). Vertical displacements of the body's CoM were used to calculate the changes in E_p , whereas the differentiation of the displacements was used to calculate changes in the CoM's speed and thus the changes of its translational kinetic energy (with horizontal and vertical kinetic components being summed up to total kinetic energy E_k). We then calculated the phase shift between E_p and E_k as the time between absolute minima of E_p and E_k divided by stride time multiplied by 360°.

2.1.1. Animals

We obtained kinematic and kinetic data from four adult quails (*Coturnix coturnix*) weighing between 180 and 240 gr. While two quails voluntarily moved across the track when released, two needed motivation (clapping or lightly tipping the tail) to move across a 3 m long walking-track at their preferred speeds. We covered the track with sand paper to reduce slipping. The

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