LIMB AND JOINT KINEMATIC CONTROL IN THE QUAIL COPING WITH STEP PERTURBATIONS

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INTRODUCTION

Our understanding of avian terrestrial locomotion has increased significantly over the past years. Still, we know little about the adaptive mechanisms used by birds to negotiate uneven locomotion.

Here we analyzed the quail, a small ground-dwelling bird, during negotiation of visible vertical drops and step-up perturbations of aprox. 10%, 25%, and 50% of their leg length.

We searched for relationships between the effective leg (a model representation) and joint kinematics. As different combinations of joint kinematics can lead to similar effective leg lengths, we can expect that their combined analysis helps to infer quail motor control goals on rough terrains.

METHODS

To better understanding of the neuromechanics of avian bipedal uneven locomotion, several quails moved on a walking-track at their preferred speeds. Uneven locomotion was analyzed by combining X-ray fluoroscopy (500 frames/sec) with 3D ground reaction forces (1 kHz). The quail negotiated visible step-up and step-down perturbations of different heights (1 cm, 2.5 cm, and 5 cm).

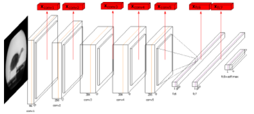


Figure 1
Model architecture and possible layer where features can be extracted

We developed semi-automated labeling method for the anatomical landmarks and automated method to estimate 3D-position of the Center of Mass. Our landmarks localization technique combines deep feature representation of the input image, landmark regression task and 3D reconstruction. Deep features are learned representations of images extracted from a Convolutional Neural Network (CNN), which serve as input to linear support vector regressors (SVR) for localizing automatically the individual landmark positions.

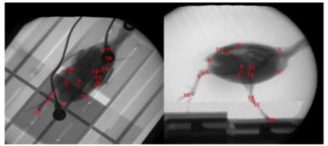
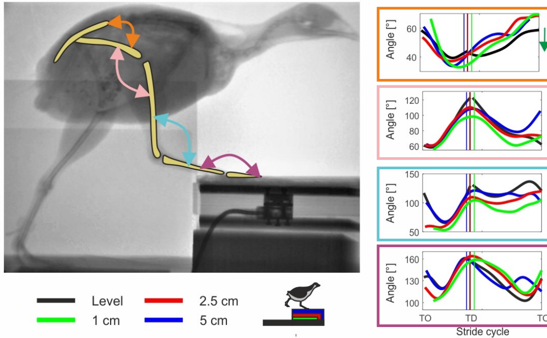


Figure 2
Semi-automated labelling of anatomic landmarks based on biplanar fluoroscopy during uneven locomotion of a quail.

RESULTS

Visible step-up perturbation



After TD on the slope, the hip was significantly more extended (larger femur retraction) than during level locomotion.

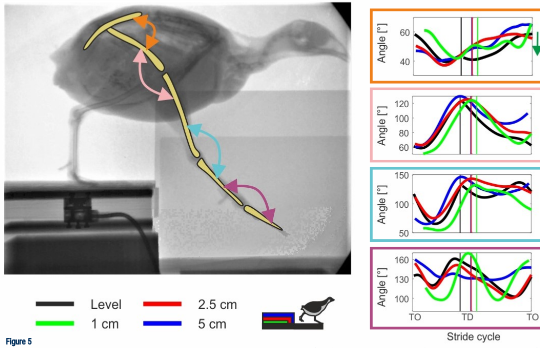
At TD, the knee joint was more flexed on the slope than during level locomotion. Excepting for 5 cm slope, the knee was mostly flexed during stance (knee is the main leg retractor). For 5 cm slope the knee showed a flexion-extension pattern (rebound) consistent with an spring-like joint behavior.

At TD, the INT was more flexed on the slope than during level locomotion. During stance, INT displayed a rebound behavior for level and for 1 cm slope, and some rebound with joint extension for 2.5 cm slope. The INT was frozen to negotiate vertical perturbations of 5 cm.

During stance, the TMTJ was mostly flexed and then extended before TO. This pattern was asociated to work absortion in the joint for level locomotion.

Figure 4
Joint angles for the hip. knee, intertarsal and metatarso-phalangeal joints in the quail during level (black) and step-up locomotion (1 cm: green, 2.5 cm: red, 5 cm: blue) . Displayed are the joint angles of the leg that step in the elevated substrate. Curves display mean values. The stride cycle comprised two consecutive leg toe-off (TO), i.e., from the end of the stance phase in step before the perturbation to the same event in the step after the vertical perturbation. Vertical solid lines indicate touch-down (TD).

Visible drop perturbation



After the drop perturbation, the hip was significantly more extended (larger femur retraction) than during level locomotion.

After a drop perturbation, the knee joint was more extended than in level locomotion. During stance, the knee was mostly flexed. For 5 cm drops, the knee showed less flexion and some rebound.

At TD, INT was more extended during perturbed than during level locomotion. During stance, INT displayed a rebound behavior for 5 cm drop. For faster drops (1 cm and 2.5 cm drops) the INT flexed, indicating work absorption.

1 cm drops induced a rebund behavior (flexion-extension pattern) in the TMTJ. For 2.5 cm drops, TMTJ patterns were similar to those observed for level locomotion. After a 5 cm drop, the TMTJ was frozen during early stance and shortly extended after midstance.

Figure 5
Joint angles for the hip. knee, intertarsal and metatarso-phalangeal joints in the quail during level (black) and step-down locomotion (1 cm: green, 2.5 cm: red, 5 cm: blue) . Displayed are the joint angles of the leg that step after the visible drop. Curves display mean values. The stride cycle comprised two consecutive leg toe-off (TO), i.e., from the end of the stance phase in step before the perturbation to the same event in the step after the vertical perturbation.Vertical solid lines indicate touch-down (TD).

Quails negotiated vertical perturbations ranging from ca. 10% to 50% leg length without major problems. None of the subjects lost visibly stability or stumbled because of the perturbations.

To overcome 1 cm vertical perturbations quails usually switched to aerial running. For negotiating 2.5 cm and 5 cm perturbations quails relied on double support phases.

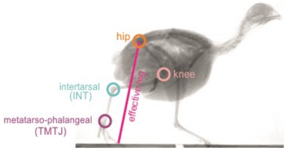


Figure 3
Joints and effective leg

DISCUSSION

We found that the quail reconfigured joint function in order to compensate for perturbations. Hip extension was used to lengthen the effective leg, while the flexion of more distal joints was used to shorten it.

For faster negotiations, the spring-like joint behavior was shifted to the most distal joint, turning the effective leg to function more spring-like than in unperturbed conditions. For more careful negotiations, the joint spring-like function is shifted towards proximal while distal joints actied as a damper or were frozen.

Interestingly, those behaviors seem to follow the same joint control goals already described for stable level locomotion in these animals. Thus, the quail appears to preserve the same overall locomotion goals despite perturbations caused by locomotion over rough terrain.

Further analysis is necessary to understand the neuromechanics underlining the viscoelastic task-shift between joints.

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