Scaling of inertial delays in terrestrial mammals

Sayed Naseel Mohamed Thangal[1], J. Maxwell Donelan[1]

[1]Department of Biomedical Physiology and Kinesiology, Simon Fraser University, Burnaby, BC, Canada

mohamedt@sfu.ca

Introduction

Inertia acts to oppose acceleration, thereby impeding changes to an animal's motion and slowing their response times. It may seem intuitive that inertia poses a bigger problem for quick responses in larger animals because, if we assume geometric similarity, total animal mass (M) is proportional to the volume of the animal whereas the muscle force needed to accelerate this mass is only proportional to muscle cross sectional area ($M^{2/3}$). The situation is even more severe for angular accelerations—moment of inertia scales with $M^{5/3}$ while muscle torque theoretically scales with M^1 (Muscle force with $M^{2/3}$ and moment arm with $M^{1/3}$). While suggestive, these scaling relationships do not correctly characterize inertial delay or its scaling for at least three reasons. First, while mass and moment of inertia of mammalian limbs scale as predicted by geometric similarity or with positive allometry (Kilbourne and Hoffman 2013), muscles and moment arms also exhibit positive allometry (Alexander et al. 1981), which could partly ameliorate the scaling of inertial effects for large animals. Second, the manner in which inertia slows movements depends upon the movement task. Third, larger animals have more time available to complete their movements (for example, they have longer stride periods and they take longer to fall to the ground).

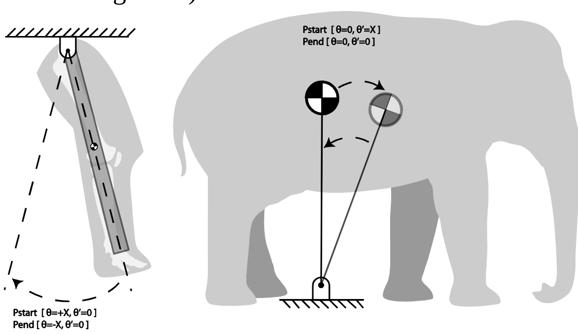

Figure 1: Figure depicting simple pendulum used to model the swing task (A) and the inverted pendulum used to model the posture task (B). Pstart indicates the starting position with Θ (angle) and Θ' (dimensionless velocity) initial conditions. Pend indicates final position.

Here we seek to understand the contribution of inertial delays to total delay and to determine how it scales with animal size. We used two simple biomechanical models to represent common tasks in animal locomotion— a simple pendulum to represent repositioning the swing limb through a specified angle (swing task), and an inverted pendulum to represent an animal controlling its posture after a perturbation (postural task). We quantified the scaling of inertial delays by scaling model parameters such as limb inertia, limb length and joint torque using measured scaling relationships from literature. We also compare the scaling and magnitude of inertial delays to the other contributing sensorimotor delays in an animal's fastest reflex response.

Methods

The swing task was modeled using a simple pendulum with distributed mass properties as shown in Fig 1. Inertial delay was defined as the time required to move from rest at a specified angle of extension (varied from 0° to 30°), to rest at the same angle in flexion. (Figure 1 A). The posture task was modeled using an inverted pendulum with point mass properties, and a zero initial angle. The system was subjected to a destabilizing forward push, modeled as an initial dimensionless velocity (varied from 0 to 0.44 $v/\sqrt{g \cdot l}$). The task was to reject this perturbation and return the system to equilibrium under muscle control, and inertial delay was the time required to do so. This task represents a quadruped mammal which was perturbed by a force which caused it to lean forward in the sagittal plane, who then returns to rest at an upright posture. The inertial properties of the simple and inverted pendulum were scaled according to Kilbourne and Hoffman (2013), while muscle force and moment arm were scaled according to mammalian non hopper values of the triceps muscle for the simple pendulum, and ankle extensor muscles for the inverted pendulum from Alexander et. al. (1981). We used optimal bang-bang control to determine the torque trajectory in both models, with the torque limits determined by the scaling of maximal muscle forces and moment arms. This control method is the fastest possible strategy for achieving the task goal, and thus represents a lower bound on delay. The models were simulated in Matlab 2016b.

Results

Inertial delays scaled less steeply (swing task: $M^{0.30}$; postural task: $M^{0.37}$) that predicted by geometric similarity (swing task: $M^{0.33}$; postural task: $M^{0.50}$). The magnitude of inertial delay depended both on the task and the size of the movement. In the swing task, the power law for inertial delay varied from $0*M^{.295}$ to $39*M^{0.292}$ milliseconds as the traversed angle increased from 0° to 60°. In the postural task, increasing the initial perturbation from 0 to 0.44 dimensionless velocity caused the power law for inertial delay to change form $0*M^{0.368}$ to $66*M^{0.400}$ milliseconds (Fig 2). For inertial delay to match sensorimotor delay, previously quantified as scaling with $33*M^{0.2}$ milliseconds (More and Donelan 2016), requires the repositioning angle to scale as $20.71*M^{-0.19}$ degrees in the swing task, and the dimensionless velocity perturbation to scale as $0.24*M^{-0.17}$ in the postural task.

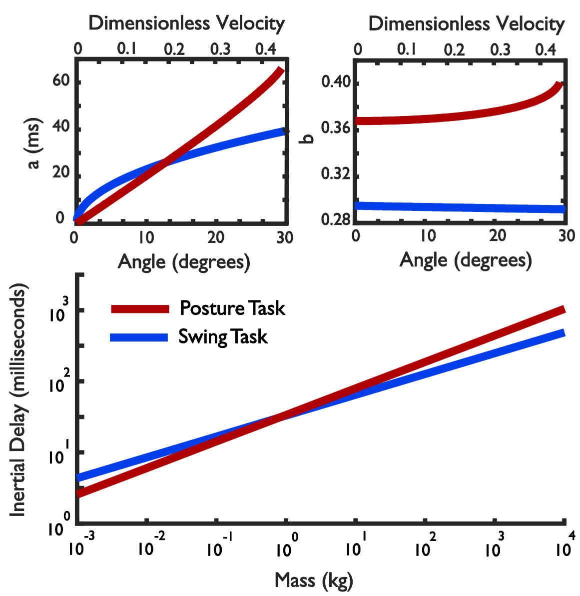

Figure 2: Graphs showing the variation in the coefficient "a" (top left) and exponent "b" (top right) of the power law (expressed as $a*M^b$), due to change in magnitude of the initial angle (swing task in blue) and dimensionless velocity perturbation (posture task in red). The bottom graph is a log-log plot of the scaling relationship between inertial delay and mass, for an initial angle of 20.72° for the swing task and a dimensionless velocity of 0.245 for the posture task.

Discussion

Our results indicate that while inertial delays scale more steeply than sensorimotor delays, its magnitude depends on task and movement size. Inertial delays in large animals begin to dominate total delay at smaller

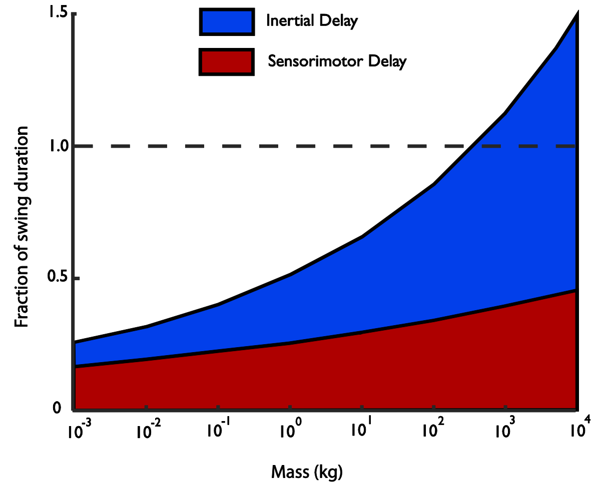

Figure 3: A semilog x axis plot representing sensorimotor delay (red) and inertial delay (blue), as a fraction of swing phase duration at the trot gallop transition speed. The inertial delay values are for 20.72°, the angle at which inertial delays equal sensorimotor delays for a 1 kg animal in the swing task.

angles, and for smaller disturbances. Inertial delays in a simulated elephant sized animal exceed sensorimotor delays for any movement greater than about 4° or any dimensionless velocity perturbation greater than 0.06. This suggests that larger animals are disproportionately burdened by inertial delay even during common movement tasks.

References

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