Scaling of rotational inertia of primate mandibles

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ABSTRACT

The relative importance of pendulum mechanics and muscle mechanics in chewing dynamics has implications for understanding the optimality criteria driving the evolution of primate feeding systems. The Spring Model (Ross et al., 2009b), which modeled the primate chewing system as a forced mass-spring system, predicted that chew cycle time would increase faster than was actually observed. We hypothesized that if mandibular momentum plays an important role in chewing dynamics, more accurate estimates of the rotational inertia of the mandible would improve the accuracy with which the Spring Model predicts the scaling of primate chew cycle period. However, if mass-related momentum effects are of negligible importance in the scaling of primate chew cycle period, this hypothesis would be falsified. We also predicted that greater "robusticity" of anthropoid mandibles compared with prosimians would be associated with higher moments of inertia. From computed tomography scans, we estimated the scaling of the moment of inertia (I_j) of the mandibles of thirty-one species of primates, including 22 anthropoid and nine prosimian species, separating I_j into the moment about a transverse axis through the center of mass (I_{xx}) and the moment of the center of mass about plausible axes of rotation. We found that across primates I_j increases with positive allometry relative to jaw length, primarily due to positive allometry of jaw mass and I_{xx}, and that anthropoid mandibles have greater rotational inertia compared with prosimian mandibles of similar length. Positive allometry of I_j of primate mandibles actually lowers the predictive ability of the Spring Model, suggesting that scaling of primate chew cycle period, and chewing dynamics in general, are more strongly influenced by factors other than scaling of inertial properties of the mandible, such as the dynamic properties of the jaw muscles and neural control. Differences in cycle period scaling between chewing and locomotion systems reinforce the suggestion that displacement and force control are more important in the design of feeding systems than energetics and speed.

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1. Introduction

Investigations of the determinants and consequences of size-related changes (scaling) in the periodicity of cyclic movements provide important insights into the design (form–function relationships) of musculoskeletal systems (McMahon, 1975; Heglund and Taylor, 1988; Biewener, 2005; More et al., 2010; Norberg and Aldrin, 2010; Hooper, 2012; Kilbourne and Hoffman, 2013). Much

of this work has focused on the scaling of step cycle period in locomotor systems (Cavagna et al., 1997; Marsh et al., 2004; Raichlen, 2004; Modica and Kram, 2005; Pontzer, 2007; de Ruiter et al., 2013), reflecting the large proportion of overall energy budgets expended on locomotion (McNab, 2002), the large proportions of locomotor energetics spent on the internal work of relative movement of limbs and trunk (Pontzer, 2007), and the importance of locomotion for foraging and predator avoidance (Reilly et al., 2007). In comparison with studies of the locomotor system, less attention has been paid to the scaling of cycle periods in the chewing system (Fortelius, 1985; Druzinsky, 1993; Gerstner and Gerstein, 2008). The chewing system provides an interesting

contrast with the locomotor system because its smaller size means that the overall energy costs of chewing are much lower than those of locomotion, suggesting that in the feeding system, optimizing energetic efficiency may be less important than optimizing control of force and displacement (Ross et al., 2009b). Here we use scaling analyses of the moment of inertia of primate mandibles—the resistance of the mandible to elevation and depression rotations during chewing—to argue that primate chew cycle period is more strongly influenced by factors such as the dynamic properties of the jaw muscles and neural control than by mandibular inertial properties. In addition, we argue that differences in cycle period scaling between chewing and locomotion systems reinforce the suggestion that displacement and force control are more important in the design of feeding systems than energetics and speed.

1.1. Scaling of mammal step cycle period

The scaling relationships between limb length and oscillation frequency are often explained with reference to pendular mechanics (for reviews see [Kilbourne and Hoffman, 2013, 2015; Kilbourne, 2014]). The cycle period of a simple pendulum (T_p)[1]—a pendulum with all its mass (M_p) concentrated at the center of mass (*CoM*) suspended at a distance L_p from the axis of rotation by a massless rod—is related to L_p and the acceleration due to gravity (g) by Equation (1).

$$T_p = 2\pi \sqrt{\frac{M_p L_p^2}{M_p g L_p}}$$

which simplifies to $T_p = 2\pi \sqrt{\frac{L_p}{g}}$

or $T_p = 2\pi \left(\frac{L_p}{g}\right)^{1/2}$ (1)

The numerator is either a torque representing the moment of inertia (resistance to rotation) of the pendulum (I_p) or L_p, a variable proportional to I_p, and the denominator is the driving torque, in this case gravity acting on pendular mass. Exponents for scaling relationships between limb step cycle periods and limb lengths that are close to ½ have often been interpreted as support for the importance of pendular mechanics in the dynamics of mammalian limbs (Pennycuick, 1975; Alexander, 2003). Importantly, however, an exponent of ½ does not require that pendular motion be driven by gravity. Indeed, not all models of limb step cycle period scaling include gravity in the denominator. McMahon's (1975) influential estimate of the scaling of the natural period of limb oscillations in galloping mammals excludes gravity driven angular momentum altogether in favor of the driving torques of the limb muscles:

$$T_0 \propto \sqrt{\frac{M_L L_L^2}{k_L b_L^2}}$$ (2)

Here, the driving torque in the denominator consists of k_L, the spring constant of the limb muscles, acting about b_L, the limb muscle lever arm. The muscle spring constant k_L is equal to $A_{pcsa} E / L_m$, where A_{pcsa} is muscle physiological cross-sectional area (PCSA), L_m is muscle length, and E is "the slope of the stress/strain curve for the stimulated muscle" (McMahon, 1975). In support of modeling muscle properties with spring constants, the spring

properties of muscles are widely acknowledged to confer not only energetic savings (McMahon, 1975; Lee and Farley, 1998), but also advantages for motor control of oscillating systems (Houk and Rymer, 1981; Nichols, 2002).

A richer understanding of the behavior of oscillating musculoskeletal systems emerges from simultaneous consideration of both gravity driven angular momentum and muscle properties in the same model. Turvey et al. (1988) presented a hybrid mass-spring/simple pendulum model in which the numerator is again the moment of inertia of a simple pendulum and the denominator includes both a gravity-driven angular momentum torque, MLg, and a muscular spring-driven torque, kb^2 (Fig. 1). The natural period of this system is described by their "equation of the pendular clocking mode":

$$T_0 = 2\pi \sqrt{\frac{ML^2}{MLg + kb^2}}.$$ (3)

Turvey et al. (1988) hypothesized that the relative importance of angular momentum and muscle properties changes with system
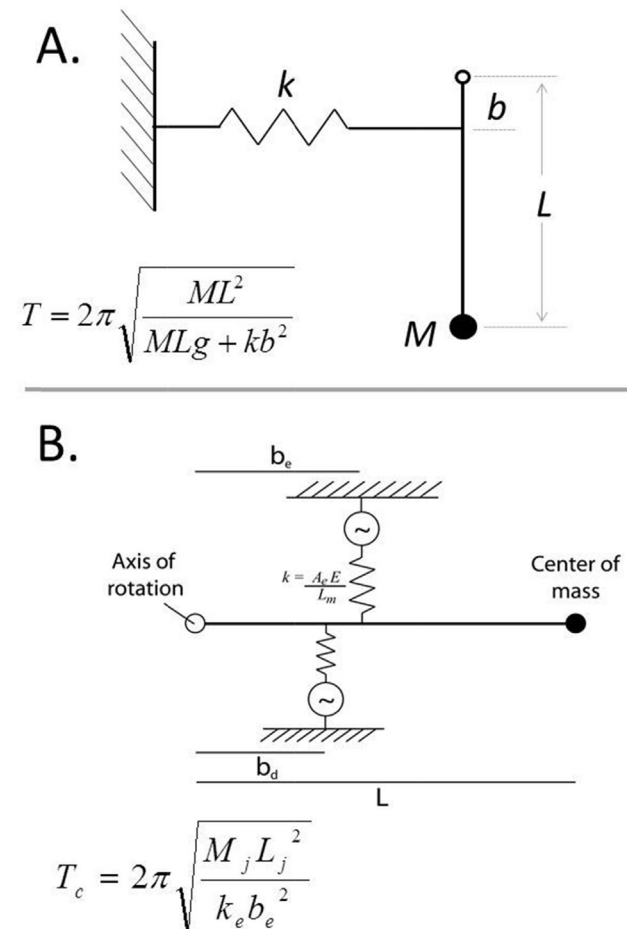

Figure 1. A. Turvey et al.'s (1988) hybrid mass-spring/simple pendulum model, together with the equation describing its natural period. The pendulum is a stiff, weightless rod of length L_p carrying a mass, M_p; a spring attached at distance b from the axis of rotation provides a restoring torque; gravity, g, acting on M at length L provides the driving torque. **B.** Spring Model of the jaw system presented by Ross et al. (2009b), together with the equation describing its natural period. L is jaw length, b_e and b_d are the jaw elevator and depressor lever arms respectively, and $k = EA_e/L_m$ is a spring constant representing the jaw-elevator muscles, where E is muscle stiffness, A_e is physiological cross-sectional area of the muscle, and L_m is muscle length (McMahon, 1975, 1984).

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[1] Fractions are used to express scaling exponents predicted by theory and decimals to express exponents estimated empirically. A complete list of abbreviations and dimensionality of terms is presented in Table 1.