



THE EVOLUTION OF LOCOMOTOR RHYTHMICITY IN TETRAPODS

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Differences in rhythmicity (relative variance in cycle period) among mammal, fish, and lizard feeding systems have been hypothesized to be associated with differences in their sensorimotor control systems. We tested this hypothesis by examining whether the locomotion of tachymetabolic tetrapods (birds and mammals) is more rhythmic than that of bradymetabolic tetrapods (lizards, alligators, turtles, salamanders). Species averages of intraindividual coefficients of variation in cycle period were compared while controlling for gait and substrate. Variance in locomotor cycle periods is significantly lower in tachymetabolic than in bradymetabolic animals for datasets that include treadmill locomotion, non-treadmill locomotion, or both. When phylogenetic relationships are taken into account the pooled analyses remain significant, whereas the non-treadmill and the treadmill analyses become

nonsignificant. The co-occurrence of relatively high rhythmicity in both feeding and locomotor systems of tachymetabolic tetrapods suggests that the anatomical substrate of rhythmicity is in the motor control system, not in the musculoskeletal components.

KEY WORDS: Coordination dynamics, locomotion, motor control.

Evolutionary neuromechanics uses comparative behavioral, physiological, and morphological data to test hypotheses about the evolution of sensorimotor systems (Nishikawa et al. 1992; Hale et al. 2002; Nishikawa 2002; Nishikawa et al. 2007; Ross et al. 2007). In this article, we test the hypothesis that high rhythmicity (low relative variance in cycle duration or period) characterizes tachymetabolic tetrapods (mammals and birds) by evaluating whether their limb movements during locomotion are more rhythmic than those of bradymetabolic tetrapods (lizards, turtles, crocodiles, and salamanders). Ross et al. (2007b) reported that mammals exhibit higher chewing rhythmicity, higher chewing frequencies, and size-related changes in chew frequency not seen in lizards (Druzinsky 1993; Ross et al. 2007; Gerstner and Gerstein 2008), and they linked these features to the higher metabolic rates of mammals (Nagy 1987, 2005), arguing that the greater energetic needs of mammals necessitate longer chewing bouts during which fatigue is avoided by more energetically efficient movements. The locomotor system provides an independent—and maybe better—test of the energetic explanation for rhythmicity because it consumes a relatively greater amount of energy than the chewing system, and because limb oscillations themselves can account for ~10% to ~33% of total locomotor cost in birds and mammals (Marsh et al. 2004; Gotschall and Kram 2005; Modica and Kram 2005; Pontzer 2007).

Our results confirm that the differences in rhythmicity between lizard and mammal chewing systems also distinguish the locomotor systems of bradymetabolic and tachymetabolic tetrapods. This suggests that these rhythmicity differences transcend musculoskeletal systems (chewing and locomotor systems) and reflect underlying differences in motor control systems. We suggest that convergently evolved specializations of the sensorimotor systems of tachymetabolic animals (birds and mammals) linked to control of temporal aspects of movement may facilitate higher rhythmicity in these clades. The association between differences in metabolic rates, kinematic rhythmicity, and sensorimotor control system design suggests a novel hypothesis regarding the evolution of motor control in tetrapods.

Materials and Methods

Locomotor rhythmicity was quantified in representative salamander, lizard, turtle, alligator, mammal, and bird species. Coefficients of variation (CV^*) of stride cycle durations (T_s) were calculated within individuals from individual limbs using $CV^* = (1 + \frac{1}{4n})CV$ (Sokal and Braumann 1980). Average intraspe-

cific values then were calculated by averaging individual CV^* s (Table 1).

Locomotor cycle durations were measured from footage of limb kinematics collected with standard (*Trachemys* and *Terrapene*) or high speed (all other taxa) video. For some taxa, multiple samples were available, including measurements collected during with and without obstacles. These different trial types provided the opportunity to test for their effects on rhythmicity. In these cases, CV^* s were calculated separately for these different cycle types (Table 1). Species average CV^* s were compared using analysis of variance (ANOVA): Games and Howell correction was used on post hoc tests when variances were non-homogeneous, Bonferroni correction was used otherwise.

Tachymetabolic and bradymetabolic species were compared using four datasets. *Treadmill data*: Data from studies of vertebrate locomotion on treadmills are of interest because species from different clades locomote under similar, albeit unnatural, conditions (Table 1). *Minimally controlled data*: Recognizing that animals do not naturally walk and run on treadmills, and that treadmill data can introduce unnatural dynamics, data from stationary substrates were also analyzed. Data were analyzed from quadrupedal locomotion of *Ambystoma maculatum* on a wet floor, *Pleurodeles waltl* on wet stainless steel (Delvolve et al. 1997), *Anolis carolinensis*, *A. sagrei*, *A. valencienni* on large wooden dowels, and primates *Cebus apella*, *Cercopithecus aethiops*, *Erythrocebus patas*, *Pan troglodytes* and, *Papio anubis* on concrete and wood floors. *Pooled substrate data*: Analyses were also performed on data from both treadmill and non-treadmill datasets combined. This enabled the broadest comparisons across taxa. Where possible, only walking data were included: although the *Alligator* and *Ambystoma* data were derived from slow trots sensu (Hildebrand 1985), they were, for our purposes, walking.

PERTURBATION DATA

The bird treadmill datasets included step cycles when turkeys (*Meleagris*), guinea fowl (*Numida*), and pheasants (*Phasianus*) were presented with obstacles of various sizes and types. The dog treadmill data included step cycles by two dogs (*Canis lupus familiaris*) with weights temporarily attached to their fore and/or hindlimbs. These datasets provided an opportunity to compare rhythmicity of birds and mammals in perturbed conditions with rhythmicity in unperturbed bradymetabolic vertebrates. This allows a conservative test of the idea that tachymetabolic vertebrates are more rhythmic, even when they are perturbed and the bradymetabolic

Table 1. Data used in this study.

Species	Treadmill (T) Non-Treadmill (N)	<i>n</i> Cycles	Mean CV*	<i>n</i> Individuals
<i>Alligator mississippiensis</i>	T	282	17.2385	4
<i>Ambystoma maculatum</i>	N	135	25.4023	5
<i>Anolis carolinensis</i>	N	198	17.5090	8
<i>Anolis sagrei</i>	N	163	18.8310	8
<i>Anolis valencienni</i>	N	138	22.8252	7
<i>Canis lupus familiaris</i> (without weights)	T	71	2.7588	4
<i>Canis lupus familiaris</i> (with weights)	T	392	2.2199	3
<i>Cebus apella</i>	N	48	11.2271	2
<i>Cercopithecus aethiops</i>	N	50	10.8846	2
<i>Coturnix coturnix</i> (no obstacles)	T	49	7.4581	2
<i>Coturnix coturnix</i> (obstacles)	T	231	11.2107	2
<i>Erythrocebus patas</i>	N	40	11.1833	3
<i>Homo sapiens</i>	T	119	1.3509	10
<i>Iguana iguana</i>	T	51	40.2379	1
<i>Meleagris carolina</i> (no obstacles)	T	50	4.6845	2
<i>Meleagris carolina</i> (obstacles)	T	114	8.2608	2
<i>Numida meleagris</i> (no obstacles)	T	60	3.9241	2
<i>Numida meleagris</i> (obstacles)	T	137	8.2342	2
<i>Pan troglodytes</i>	N	33	7.3252	2
<i>Papio anubis</i>	N	174	13.2701	2
<i>Phasianus colchicus</i> (no obstacles)	T	24	4.6618	2
<i>Phasianus colchicus</i> (obstacles)	T	24	9.4749	2
<i>Pleurodeles waltl</i>	N	104	15.6791	1
<i>Pseudemys concinna</i>	T	169	14.8291	3
<i>Sus scrofa</i>	T	30	6.4481	2
<i>Terrapene carolina</i>	T	67	9.6427	1
<i>Trachemys scripta</i>	T	332	18.2316	3
<i>Tupinambis merianae</i>	T	23	15.6229	2
<i>Varanus exanthematicus</i>	T	68	20.2769	1

vertebrates are not. Data were also available from *Ambystoma* individuals walking on a wet tank floor versus walking in water, allowing examination of effects of these substrates on variance.

To quantify the amount of phylogenetic signal in our data, values for κ (Blomberg et al. 2003) and Pagel's λ were calculated for T_s CV* across the full phylogeny using R (Revell 2012). Despite significant phylogenetic signal in our data, analyses were performed both using species means without taking phylogenetic relationships into account ("tips" analyses) as well as in an explicit phylogenetic context (Felsenstein 1985; Harvey and Pagel 1991; Garland et al. 1993). We took the phylogenetic relationships among the species into account by creating an empirical null distribution of F -values using the phylogenetic relationships among the species and using this to calculate a phylogenetically corrected critical F -value (F_{PHYLCrit}). Observed F -values were compared with those from a standard F -distribution (F_{TIPS}) and with F_{PHYLCrit} . Phylogenetic branching pattern and branch lengths (Fig. 1) were derived from the following (Stephens and Wiens 2003, 2008; Hugall et al. 2007). Where specific branch depths were not available, unknown branch lengths were divided evenly

between known divergence times and the present. Using this tree, we used the PDSIMUL program (Garland et al. 1993) to simulate the evolution of T_s CV*. We used a Brownian motion model of evolutionary change across 1000 simulations with the means and variances of each simulation set to those of the tip data. These simulations were then brought into the software PDANOVA (Garland et al. 1993) where a traditional one-way ANOVA was performed on each of the 1000 simulations and the F -value for each simulation was saved. F_{PHYLCrit} was set as the F -value of the 95th percentile of this distribution. Results of analyses of both "tips" and phylogenetically "corrected" data are reported.

Results

κ AND PAGEL'S λ

The values of κ and λ for T_s CV* across the whole dataset were: $\kappa = 0.461$, $P = 0.003$; $\lambda = 0.771$, $P = 0.005$. There is significant phylogenetic signal in the data. This is reflected in differences between results from analyses of "tips" versus phylogenetically corrected data.

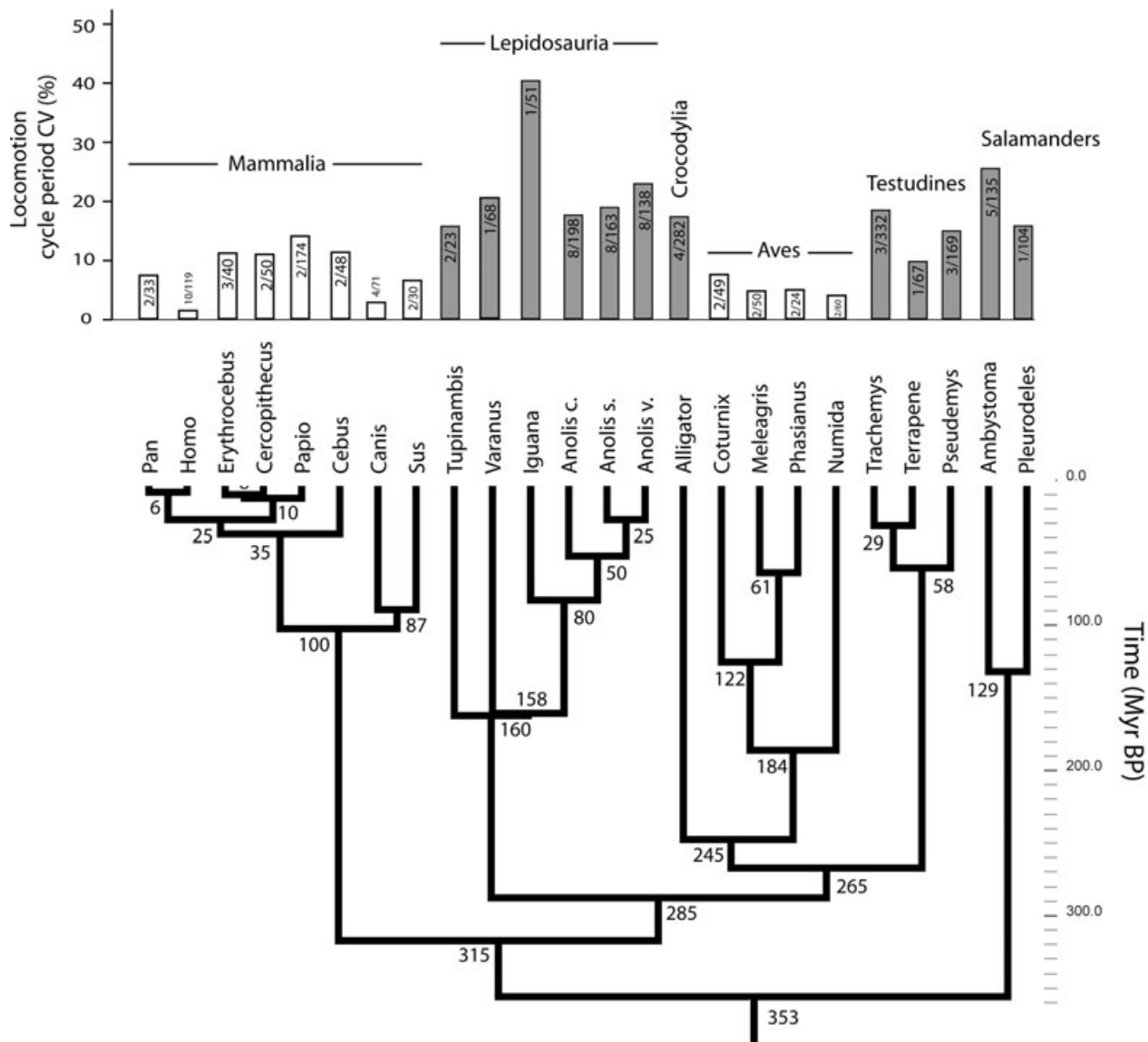


Figure 1. Phylogeny of species used in this study with branch point dates in millions of years before present (Myr BP) and bar graph of average coefficients of variation (CV*) of locomotor cycle period for each species. CV*s were calculated within individuals from three or more sequential strides at walking or walk-trot gaits. Numbers on bars are numbers of individuals/number of stride cycles. Blomberg et al.'s $\kappa = 0.492$, $P = 0.003$; Pagel's $\lambda = 0.814$, $P = 0.004$ (Pagel 1999; Blomberg et al. 2003).

POOLED SUBSTRATE ANALYSES

All mammal and bird species exhibit lower mean T_s CV*s (stride cycle duration CV*s) than all lizards, alligators, and salamanders, and all turtles except *Terrapene*. *Terrapene* had a lower mean T_s CV* than the primates sampled (Fig. 1). Using pooled treadmill and non-treadmill data, average T_s CV* for tachymetabolic tetrapod species (mean = 7.2, $n = 12$ species) is significantly lower than that for bradymetabolic tetrapods (mean = 19.7, $n = 12$ species) ($F_{TIPS} = 25.0$, $P < 0.001$). This difference is still significant when a phylogenetically corrected F -value is used ($F_{PHYLCrit} = 24.7$, $P < 0.05$).

TREADMILL ANALYSES

Using treadmill data, tachymetabolic tetrapod species have lower mean T_s CV*s (5.5, $n = 8$) than bradymetabolic tetrapod species (T_s CV* = 19.4, $n = 7$; Fig. 2). This difference is significant when "tips" data are used ($P = 0.002$), but F_{TIPS} (13.8) is slightly below that required for significance at a 0.05 level in a phylogenetic context ($F_{PHYLCrit} = 14.4$; i.e., is not significant).

MINIMALLY CONTROLLED ANALYSES

When non-treadmill data are used, tachymetabolic tetrapod species have a lower average T_s CV*s (11.01, $n = 5$) than

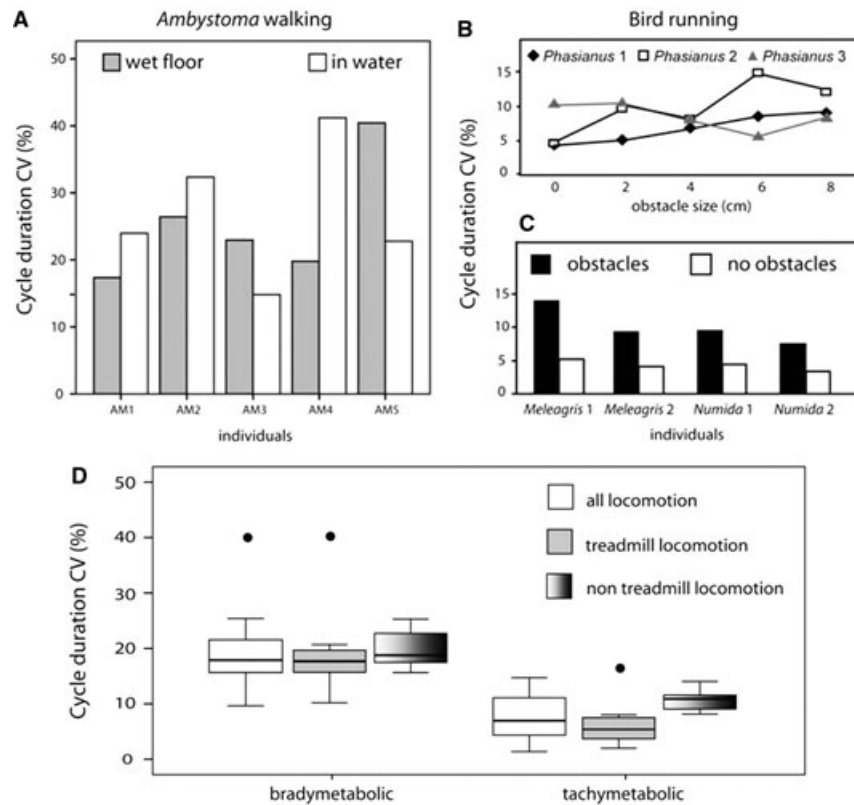


Figure 2. Results of analyses of cycle duration variance. Clockwise from top left. (A) Cycle period CV*s for five individuals of the lissamphibian *Ambystoma maculatum* locomoting on a wet tank floor or with their bodies partly suspended in water. There is no consistent effect of substrate on levels of variance in *Ambystoma*. (B) Effects of obstacle size on CV* of locomotor cycle period in pheasants running on treadmills. In two of three animals, increases in obstacle size are associated with increases in CV*. (C) Effect of obstacles on CV* in bird locomotion. In the two *Meleagris* (turkeys) and two *Numida* (Guinea fowl) studied presence of obstacles was associated with increases in CV*, but these birds still had lower locomotor CV*s than tachymetabolic animals walking on treadmills. (D) Box plots of cycle period CV*s for bradymetabolic and tachymetabolic species. Outliers indicated by dots. Analyses of the data using species-level “tips” data showed that cycle duration CV* is significantly lower in tachymetabolic than in bradymetabolic animals using treadmill data, non-treadmill data, or pooled treadmill and non-treadmill data. When phylogenetic relationships of the species were taken into account, the pooled substrate analysis remained significant, the treadmill data become nonsignificant (but only marginally) and the non-treadmill data were not significant.

bradymetabolic tetrapods (T_s CV* = 20, $n = 5$; $F_{TIPS} = 15.5$, $P = 0.004$). This difference is not significant using a phylogenetically adjusted F -value ($F_{PHYLcrit} = 91.4$, $P > 0.05$).

PERTURBATION ANALYSES

When comparisons were made using treadmill and non-treadmill data combined, bird species confronted by obstacles had lower average T_s CV*s (10.3, $n = 4$) than bradymetabolic species (mean = 19.4, $n = 7$). This difference is significant using tips data ($F_{TIPS} = 5.8$, $P = 0.03$) but not in a phylogenetic context ($F_{PHYLcrit} = 16.4$, $P > 0.05$). This difference was not significant when only treadmill data were used (i.e., excluding *Anolis* on large dowels and *Ambystoma* on wet tank floors; $F_{TIPS} = 3.3$, $P = 0.17$). The two dogs with weights of varying amounts attached to their limbs had lower average T_s CV*s (2.1, $n = 2$) than bradymetabolic animals (mean = 19.4, $n = 7$). This difference is significant using

tips data ($t_{TIPS} = 2.2$, $P = 0.048$), but not using phylogenetically corrected data.

Different-sized obstacles were presented to three pheasants (*Phasianus*) running on a treadmill. Two out of three pheasants showed increases in variance with obstacle size (Fig. 2). In addition, for turkeys (*Meleagris*) and guinea fowl (*Numida*), when cycles that included obstacles were pooled with the cycle immediately after, these cycle durations were more variable than cycles that lacked obstacles (Fig. 2). Three *Ambystoma* exhibited higher variance when walking in water and two showed higher variance when walking on a wet tank floor (Fig. 2).

Discussion

This study compared rhythmicity of locomotor movements among tetrapods to evaluate whether differences in rhythmicity between

mammal and lizard feeding systems are also found in the locomotor system and whether tachymetabolic tetrapods (birds and mammals) are more rhythmic than bradymetabolic tetrapods (lizards, alligators, turtles, salamanders). Analyses of the species-level “tips” data confirmed that variance in locomotor cycle periods is significantly lower in tachymetabolic than in bradymetabolic animals using treadmill data, non-treadmill data, or pooled treadmill and non-treadmill data. When phylogenetic relationships of the species were taken into account, the pooled substrate analysis remained significant, the treadmill data become marginally nonsignificant and the non-treadmill data were not significant. Birds confronted with obstacles and dogs with weights added to their limbs had less variable cycle durations than bradymetabolic species when using data from both treadmill and non-treadmill substrates, but these differences do not survive phylogenetic correction. The loss of significance using phylogenetically “corrected” *F*-values reflects loss of degrees of freedom due to phylogenetic relatedness; that is, if closely related species are assumed to not represent independent data points, there are only two tachymetabolic clades with which to test our hypotheses (Felsenstein 1985; Fig. 1). This effect is reflected in our data by significant values of κ and Pagel’s λ (Revell 2012). Our analyses are also impacted by the diversity of locomotor types encompassed by our sample. This makes it difficult to define dynamically similar conditions across, for example, sprawling and para-sagittal gaits. Similarly, at present it is not possible to meaningfully test whether differences in variance are related to differences in average frequency. Are faster systems naturally less or more variable than slower systems? However, we do point out that the higher rhythmicity of mammals is seen across both chewing and locomotor systems, and across the whole range of system sizes, from the 19 mm long mandibles of chewing shrews, oscillating at 9 Hz, to the 600-mm-long limbs of running dogs, oscillating at 2 Hz. Despite these limitations with our data, the large magnitude of the differences in variance between tachymetabolic and bradymetabolic tetrapods in locomotor cycle durations and the persistence of these differences across multiple lineages of birds and mammals suggests that these clade-specific differences in rhythmicity could be important and selectively advantageous.

What is the functional significance of these differences in rhythmicity between tachymetabolic and bradymetabolic tetrapods?

FUNCTIONAL ADVANTAGES OF HIGH RHYTHMICITY

The data presented here support the hypothesis that differences in rhythmicity of cyclic behaviors are related to metabolic rate (Ross et al. 2007): tachymetabolic tetrapods locomote more rhythmically than bradymetabolic tetrapods. Energetic efficiency is also hypothesized to underlie the scaling of cycle durations that are documented within and between species of birds and

mammals, but are not reported for bradymetabolic tetrapods (McMahon 1975; Heglund and Taylor 1988; Biewener 1990; Druzinsky 1993; Raichlen 2004; Gerstner and Gerstein 2008).

Another function of high rhythmicity may be to facilitate locomotion control. Unstable dynamic states are characterized in part by increased variability (Guckenheimer and Holmes 1997; Full et al. 2002; Holmes et al. 2006), and nonlinear state changes in musculoskeletal systems such as these are monitored by the central nervous system (Kelso 1995; Meyer-Lindenberg et al. 2002; Aramaki et al. 2006; Jantzen et al. 2009; Kelso 2010) at the cost of attention to other stimuli (Monno et al. 2000; Zanone et al. 2001). This suggests that the dynamically unstable, less rhythmic states, like those preceding gait transitions, are noisier and less predictable than steady-state movement, and therefore may be more dangerous, or more difficult and energetically costly to control. In this context, gait changes may represent predictive, anticipatory switching of movement types to minimize these effects (Goodman et al. 2000; Levy-Tzedek et al. 2011). Thus, we hypothesize that one of the most important advantages of higher kinematic rhythmicity is greater temporal predictability of kinematic events (Ross et al. 2007). The principle advantage of temporal predictability is improved *coordination* of oscillating musculoskeletal and nervous components. Coordination—the “ability to maintain a context-dependent and phase-dependent cyclical relationship between different body segments or joints in both spatial and temporal domains” (Krasovskiy and Levin 2010)—is achieved in part through phase synchronization: the locking of phases of coupled oscillators irrespective of oscillation amplitude (Boccaletti et al. 2002). Salient examples of phase synchronization of vertebrate cyclic movements include: tuning of locomotor and ventilation systems in tetrapods (Nassar et al. 1996); phase synchronization of jaw and tongue oscillations in mammals (Hiiemae 1978; Bramble and Wake 1985); phase synchronization of limb oscillations (Prochazka et al. 2002); coordination of reaching and obstacle avoidance with ongoing locomotion (Drew et al. 2002, 2004, 2008); and synchronization of oscillating neural systems with the oscillating musculoskeletal structures (Verdaasdonk et al. 2006).

WHAT IS THE NEURAL SUBSTRATE FOR DIFFERENCES IN RHYTHMICITY?

Three components of the sensorimotor system that have evolved convergently in birds and mammals are plausibly linked to the evolution of rhythmicity: large Ia afferents from muscle spindles, γ -motoneuron innervation of muscle spindles, and enlarged and elaborated cerebella and telencephala.

Mammal and bird spindle Ia afferents are distinguished from those of other vertebrates by their large, myelinated axons, facilitating rapid conduction of spindle afferent information to the central nervous system (CNS; Matthews 1972; Prochazka et al.

2002; Romanovsky et al. 2007b). Theoretical studies show that afferent information is crucial for matching the resonance of central pattern generators (CPGs) to that of the musculoskeletal system (Verdaasdonk et al. 2006) and that the stronger the afferent proprioceptive signal, the more stable the frequency output (Ausborn et al. 2007). Complete de-afferentation of spinal cord CPGs results in variable locomotor rhythms, disrupted coordination, and inability to compensate for variation in external forces and displacements (Grillner and Zangger 1974, 1975; Wetzel et al. 1976; Grillner and Zangger 1984; Allum et al. 1998).

All tetrapods share intrafusal (within-spindle) contractile elements that function to maintain spindle responsiveness during shortening. Mammals and birds are distinctive in having γ -motoneurons (γ -MNs, fusimotor neurons) from the CNS that are independent of motor supply to the extrafusal fibers (Bilo et al. 1980; Maier 1992a, b; Romanovsky et al. 2007a). The functional significance of γ -MNs in birds is unstudied, but γ -MNs in mammals facilitate anticipatory, predictive sensorimotor gain control, also called “fusimotor set” (Prochazka et al. 1985). This would provide a mechanism whereby appropriate descending commands can be used to match spindle response properties to *anticipated* variation in substrate compliance and orientation, thereby decreasing the sensitivity of the motor system to variation in the external environment.

In addition to large Ia afferents and γ -MNs, birds and mammals have also convergently evolved relatively enlarged lateral cerebella (Butler and Hodos 2005), along with larger and more complex input and output nuclei (Appelberg et al. 1975; Johansson 1988; ten Donkelaar 1988; Wild and Williams 2000). The cerebellum is an important locus of control for temporal aspects of behavior (Ivry et al. 2002; Spencer et al. 2003; Bares et al. 2009), including predictive and online correction for external disturbances (Scheidt et al. 2012).

Conclusions

Clade-specific variation in movement rhythmicity suggests mammals and birds execute cyclic oscillations of musculoskeletal systems more rhythmically than other tetrapods. This is true of both feeding and locomotor systems, and is most parsimoniously viewed as a case of convergent evolution: high rhythmicity evolved independently in the stem lineages of extant mammals and birds. We hypothesize that high rhythmicity in mammals and birds is part of a suite of features of the sensorimotor system that enhance predictive motor control to minimize effects of external perturbations, and synchronize and coordinate oscillations of multiple components of sensorimotor systems. Mammals and birds are also tachymetabolic, so rhythmicity may be functionally related to higher energy demands, suggesting that rhythmicity and predictive motor control may help avoid or postpone fatigue.

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