

# Locomotor head movements and semicircular canal morphology in primates

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**Animal locomotion causes head rotations, which are detected by the semicircular canals of the inner ear. Morphologic features of the canals influence rotational sensitivity, and so it is hypothesized that locomotion and canal morphology are functionally related. Most prior research has compared subjective assessments of animal “agility” with a single determinant of rotational sensitivity: the mean canal radius of curvature ( $R$ ). In fact, the paired variables of  $R$  and body mass are correlated with agility and have been used to infer locomotion in extinct species. To refine models of canal functional morphology and to improve locomotor inferences for extinct species, we compare 3D vector measurements of head rotation during locomotion with 3D vector measures of canal sensitivity. Contrary to the predictions of conventional models that are based upon  $R$ , we find that axes of rapid head rotation are not aligned with axes of either high or low sensitivity. Instead, animals with fast head rotations have similar sensitivities in all directions, which they achieve by orienting the three canals of each ear orthogonally (i.e., along planes at 90° angles to one another). The extent to which the canal configuration approaches orthogonality is correlated with rotational head speed independent of body mass and phylogeny, whereas  $R$  is not.**

angular velocity | vestibular

The inner ear contains three bony semicircular canals, each of which encloses an endolymph-filled duct. Head rotations during locomotion cause inertial endolymph movements that are communicated to the brain. Canal morphology affects endolymph flow and thus influences an animal's sensitivity to rotation; if an animal is more sensitive to rotations about some axes than others, and if different patterns of head rotation are produced by different locomotor behaviors, then canal morphology and locomotion could be functionally related. By this reasoning, differences in canal morphology in living and extinct animals have been attributed to interspecific differences in locomotion (1–10), but characterization of any functional relationship between canal morphology and locomotion has been limited by the use of simplified models of canal sensitivity and the absence of in vivo data about how the head actually moves (11).

The relevant variables for comparing canal sensitivity with head movement are angular velocity vectors and vestibular sensitivity vectors, respectively. (Although the direct stimulus to the canal is angular acceleration, the canal response is proportional to angular velocity within a range of head movement frequencies. Angular velocity was used here for a variety of reasons, as described in *SI Materials and Methods*.) Angular velocity vectors characterize instantaneous head rotations about different axes and can be experimentally measured in moving animals. Vestibular sensitivity vectors characterize the extent to which an animal is more sensitive to rotations about some axes than other axes. Although vestibular sensitivity vectors cannot be measured directly, they can be estimated from canal morphology. Specifically, a canal's sensitivity to a rotation about any axis can be expressed as a vector, wherein vector magnitude indicates the amount of endolymph movement resulting from rotation about the vector axis. The amount of endolymph movement is determined by the canal radius and by the

angle between the rotational axis and a plane describing the orientation of the canal (12–15). Because an animal has three canals in each inner ear, an animal's overall vestibular sensitivity to a rotation is the vector sum of the six canal sensitivities (14, 16).

Previous studies have used the morphological variable  $R$  (the mean radius for the three canals in each ear) as a proxy for vestibular sensitivity and have used field-observational impressions of movement, such as “agility rank” as a proxy for angular velocity. However,  $R$  increases with negative allometry with respect to body size (1, 17), leading to radically different interpretations of the significance of variation in  $R$ . Some have reasoned that, because large animals appear to have slower movements than smaller animals, high sensitivity (absolutely large  $R$ ) is adaptive for detecting slow head rotations (1, 18). In contrast, seemingly fast-moving species exhibit greater  $R$  measurements than slower species of similar body size. As a result, others suggest that high sensitivity (relatively large  $R$ ) is adaptive for detecting fast head rotations (2, 17).

We compared vector measurements of angular velocity and vestibular sensitivity in a model group of 11 strepsirrhine (lemur and loris) primate species (Table 1). We chose to work with this sample for several reasons. (i) Statistical methods that correct for the evolutionary relatedness of sample taxa [e.g., phylogenetic generalized least-squares (PGLS) regression] are most sensitive when the sample includes closely related species with widely divergent traits (19). (ii) Strepsirrhine primates exhibit extreme interspecific variation in body size through three orders of magnitude (~0.05 kg to ~5 kg). (iii) Strepsirrhines engage in an exceptionally wide range of locomotor behaviors (20). For example, the mouse-sized *Microcebus* scampers on all fours; rat-sized *Galago* moves by ricochet orthograde, jumping like a tiny kangaroo; *Nycticebus* is called a “slow loris” because of its sloth-like movements; cat-sized *Lemur* is primarily a terrestrial quadruped; and the large *Propithecus* is an orthograde specialist that moves by graceful bipedal leaping. Finally, (iv) strepsirrhine locomotor diversity has been thoroughly studied both in captivity and the wild (21–26), which allowed us to provide the appropriate indoor supports and environments necessary for animals to perform naturalistic locomotor behaviors (see *Materials and Methods* for details).

## Results

In 3D kinematic experiments, we sampled angular head velocities at 120 Hz. Each animal wore a cap bearing reflective markers, and data were acquired while the animal moved freely. Head rotations were sampled during six categories of locomotor behavior: terrestrial walking, terrestrial running, arboreal support walking, horizontal support leaping, vertical support leaping, and bipedal

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**Table 1. Number of gait cycles analyzed per species and study behavior**

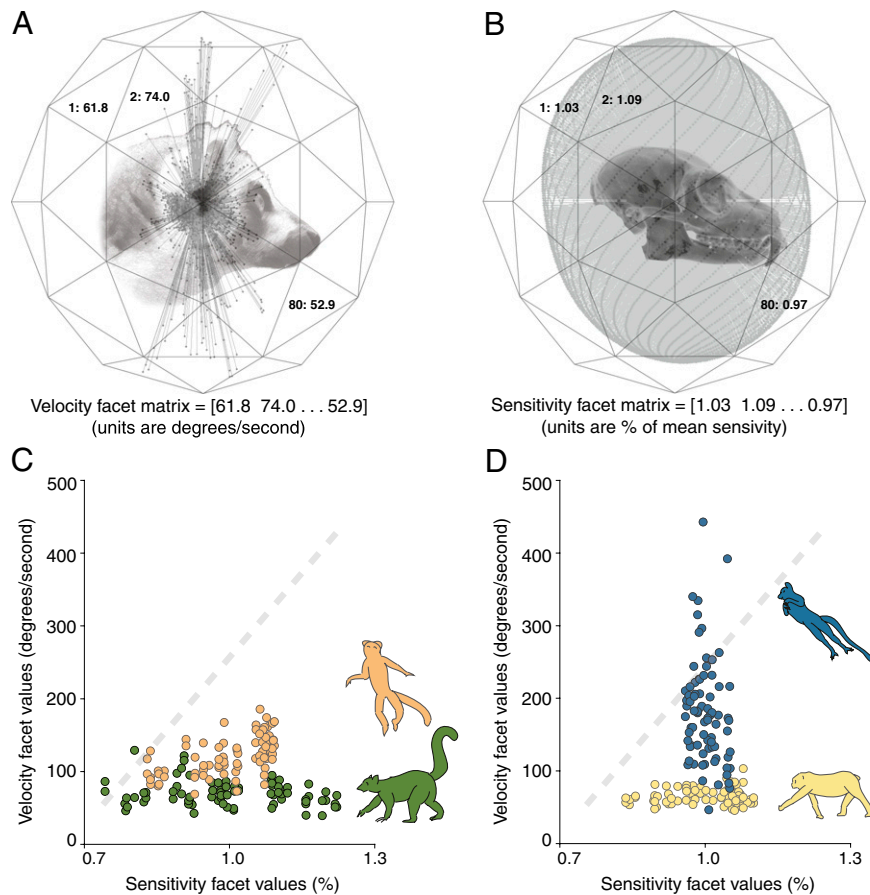
Species	n	AW	HL	TR	TW	BL	VSL
<i>Cheirogaleus medius</i>	2	31		35	15		
<i>Daubentonia madagascariensis</i>	2	27	11	14	18		
<i>Eulemur fulvus</i>	3		3	20	9		
<i>Eulemur mongoz</i>	2	18	12	22	17		
<i>Galago moholi</i>	2	8				8	11
<i>Hapalemur griseus</i>	2	14	6	30			16
<i>Lemur catta</i>	3	27	14	23	22		
<i>Microcebus murinus</i>	2	4		42	3		
<i>Nycticebus pygmaeus</i>	2	34			51		
<i>Propithecus verreauxi</i>	2					16	22
<i>Varecia variegata</i>	3	7	8	21	12		

The second column lists the number of animals used from each species. Study behaviors: arboreal walking (AW), bipedal leaping (BL), horizontal leaping (HL), terrestrial running (TR), terrestrial walking (TW), and leaping among vertical supports (VSL).

leaping (Table 1). The ranges and means of our angular head velocity measurements were comparable to the limited existing data from anthropoid primates and other mammals (Table S1,

single-behavior means of angular velocity magnitude) (11, 27–29). CT scans of skulls (Table S2) were used to measure each canal's radius and plane of orientation (16, 30), which can be used to calculate canal sensitivity to rotations about different axes (14). For each specimen, the vestibular sensitivity was calculated for rotations about axes spaced at 1° intervals in all directions (16).

The existing hypotheses outlined above predict that axes of high vestibular sensitivity should align with axes of either fast rotation or slow rotation. To test for such alignment, we paired angular velocity and vestibular sensitivity vectors by orientation and then treated the magnitudes of the paired vectors as  $x$  and  $y$  variables in a bivariate plot. Positive significant correlations would suggest that sensitive canals are adaptive for detecting fast head rotations, whereas negative significant correlations would suggest that sensitive canals are adaptive for detecting slow head rotations. To facilitate such pairings, we divided an imaginary sphere surrounding the head into equal facets and then calculated the mean magnitude of vectors pointing toward each facet. The resulting mean magnitudes were output as a facet matrix, wherein row number identified the 3D location of the facet from which the row's identity was calculated (Fig. 1 *A* and *B*). When applied to a vestibular sensitivity vector set and to an angular velocity vector set from the same species, the resulting sensitivity and velocity facet matrices were paired by row.

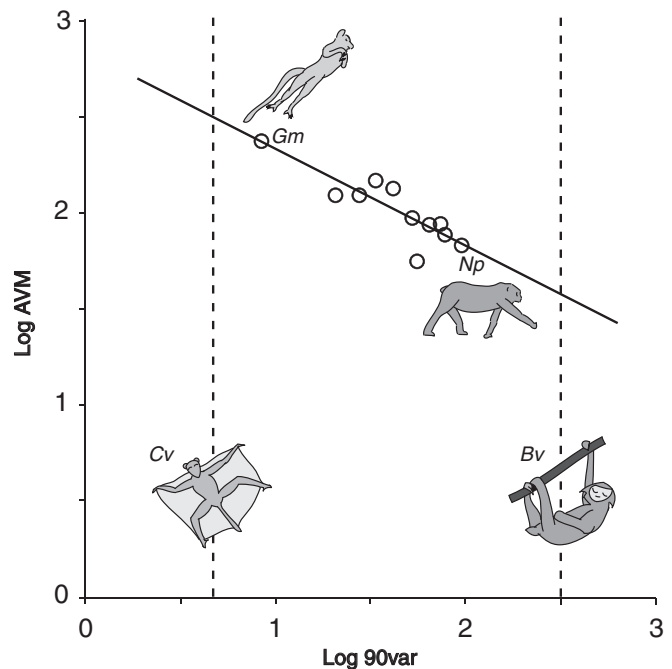


**Fig. 1.** (*A*) Angular velocity vectors from terrestrial walking in *Lemur catta*. An 80-facet icosahedron envelops the data. Each facet is associated with two numbers: the first number identifies the facet location and the second number is the mean magnitude of vectors pointing to the facet. A velocity facet matrix is constructed below. (*B*) Vestibular sensitivity vectors predicted from a CT scan of *L. catta*. Vectors are calculated at 1° increments and appear as an ovoid cloud. A sensitivity facet matrix is constructed below. (*C*) Summary of all data for *Hapalemur griseus* (orange), which employs orthograde leaping, and size-matched *Eulemur mongoz* (green), which is more quadrupedal. (*D*) Summary of all data for *Galago moholi* (blue), which leaps bipedally, and size-matched *Nycticebus pygmaeus* (yellow), a slow quadruped. Comparisons in *C* and *D* illustrate that animals with fast rotations have less variation in sensitivity (tall and narrow distribution for *G. moholi*), whereas animals that rotate slowly have more variation in sensitivity (low and wide distribution for *N. pygmaeus*). These data conflict with predictions that axes of fast rotation should align with axes of high or low sensitivity (gray expected trendline and its inverse, respectively).

Contrary to the predictions of the existing hypotheses, intra-specific correlations between sensitivity and velocity facets were not consistently positive and significant, or negative and significant (Table S3). That is, our experimental data suggest that axes of high sensitivity do not align with axes of fast rotation or with axes of slow rotation. Instead, we found that species exhibiting fast rotations about any axis have less overall variation in vestibular sensitivity, whereas species exhibiting slow rotations about all axes have more overall variation in vestibular sensitivity (Fig. 1 C and D). PGLS regression confirms that variation in vestibular sensitivity magnitude was negatively correlated with mean angular velocity ( $R^2 = 0.63$ ,  $P < 0.01$ ). To further explore this unique finding, we tested for correlations between variables reflecting overall rotational head speed (i.e., variables calculated from angular velocity magnitudes) and the three distinct anatomic features that determine directional variation in vestibular sensitivity magnitude. Specifically, if each of an animal's six canals has an equal radius, and if each canal is oriented at  $90^\circ$  or  $180^\circ$  to every other, the vestibular sensitivity will be equal in all directions (14). Thus, we hypothesized that variance from  $90^\circ$  among angles between canals of one side of the head (90var), variance from  $180^\circ$  among angles between canals of opposite sides (180var), or variance in radius among all six canals (Rvar) should be less in species with relatively fast overall rotational head speed.

Because we measured head rotations during multiple behaviors in each species, there were many possible ways to construct a variable reflecting rotational head speed. If natural selection is acting on vestibular sensitivity, the canals could be shaped to: (i) optimize overall fitness for a variety of locomotor modes used during the animal's lifespan or, (ii) meet the demands of especially "risky" locomotor behaviors (e.g., those forms of locomotion most likely to cause self-injury that would reduce fitness). To examine the first possibility, for each species, we constructed a weighted mean of angular velocity magnitude (AVM) from the mean angular velocities produced by each study behavior adjusted for the percentage of time the species engages in each behavior, as determined from published field studies (Tables S1 and S4–S7) (21, 23, 24, 26). PGLS regressions were used to examine if our three functionally related measurements, Rvar, 180var, or 90var, are significantly correlated with AVM or the average body mass of the species (Table S8). The effects of body mass were examined because canal radius is known to scale with body mass (1). Although Rvar approaches significant correlation with AVM ( $P = 0.054$ ), 90var is strongly correlated with AVM ( $P < 0.001$ ) and is not correlated with body mass ( $P = 0.252$ ). A least-squares regression of AVM versus 90var approximates the PGLS regression results and visually conveys the strength of the relationship in strepsirrhine primates (Fig. 2).

The second alternative possibility that the canals are shaped to meet the demands of "risky" locomotor behavior (as defined above) proved difficult to evaluate. Two variables intended to reflect rotational head speed during risky behaviors were calculated, and both, like AVM, were significantly correlated with 90var. One approach would have been to calculate rotational head speed using data sampled from seemingly risky behaviors. However, it is not clear if it is riskier for *Haplemur* to leap bipedally or quadrupedally, or how this should compare with the obligate bipedal leaping of *Propithecus*, or even what should be considered a risky behavior for *Nycticebus*, which has never been reported to leap. Moreover, the relationship between apparent risk and angular velocity magnitude is not as simple as might be assumed. Whereas, for most taxa, terrestrial running seems riskier and produces faster head rotations than terrestrial walking, arboreal walking seems riskier but produces slower head rotations than terrestrial walking (Table S1, single-behavior means of angular velocity magnitude). Assuming that faster head rotations were associated with some degree of greater risk of injury than slow head rotations within a given locomotor behavior,



**Fig. 2.** AVM and 90var in primates, with evidence that this relationship may also be true for other mammals. Points for fast-leaping *G. moholi* (Gm) and the conspicuously slow *N. pygmaeus* (Np) are at the low and high extremes of the primate 90var range, respectively. A line fit to the primate data predicts plausible AVM values from 90var measurements of the nonprimate taxa *C. volans* (Cv) and *B. variegatus* (Bv).

we calculated weighted means from both the fastest quartile and from the single fastest rotation measured during each locomotor behavior. In PGLS regressions, the variable based on the fastest quartile of head rotations was almost as strongly correlated with 90var as was AVM ( $R^2 = 0.75$ ,  $P < 0.001$ ), but the variable based on the single fastest rotation was not as strongly correlated with 90var ( $R^2 = 0.65$ ,  $P = 0.001$ ). In summary, all rotational head speed variables were significantly correlated with 90var. Recognizing that selection could shape the canals to match demands characterized by more than one of the available rotational head speed variables, we arbitrarily chose to work with AVM alone in ensuing analyses.

To assess whether AVM and 90var might be correlated in other mammals more generally, we measured the semicircular canals of two nonprimate species with very different locomotor modes: *Cynocephalus volans* (the colugo, a gliding mammal) and *Bradypus variegatus* (a sloth) (2). We found that 90var for the gliding mammal was less than, and that 90var for the sloth was greater than, any of the 90var measurements for the primates in our sample (Fig. 2). This result suggests that the correlation between 90var and AVM established here for strepsirrhine primates may be cautiously extrapolated to other mammals.

Finally, we tried to optimize an equation for inferring AVM in extinct primates. Using PGLS regressions, conventional morphologic variables ( $R$  and body mass, BM) and newly defined morphologic variables (90var and Rvar) were ordered from most-to-least correlated with AVM (Table S9). Only 90var was significantly correlated with AVM; Rvar approached significant correlation with AVM; body mass and  $R$  were not significantly correlated with AVM. The correlation coefficient for a multivariate equation predicting AVM from 90var and Rvar together is negligibly greater than that for the equation predicting AVM from 90var alone (Eqs. 1 and 2). A multivariate equation estimating AVM from body mass and  $R$  is not significant (Eq. 3), and any AVM predicted from Eq. 3

would depend largely upon the body mass estimate used. Eq. 1 is size-independent and may be expository for predicting AVM in extinct species.

$$\text{Log}_{10}\text{AVM} = -0.51(\text{Log}_{10}90\text{var}) + 2.83 \quad [1]$$

$$(R^2 = 0.76, p < 0.001)$$

$$\text{Log}_{10}\text{AVM} = -0.46(\text{Log}_{10}90\text{var}) - 0.07(\text{Log}_{10}R\text{var}) + 2.66 \quad [2]$$

$$(R^2 = 0.77, p < 0.001)$$

$$\text{Log}_{10}\text{AVM} = -0.31(\text{Log}_{10}\text{BM}) + 1.08(\text{Log}_{10}R) + 2.63 \quad [3]$$

$$(R^2 = 0.34, p = 0.060)$$

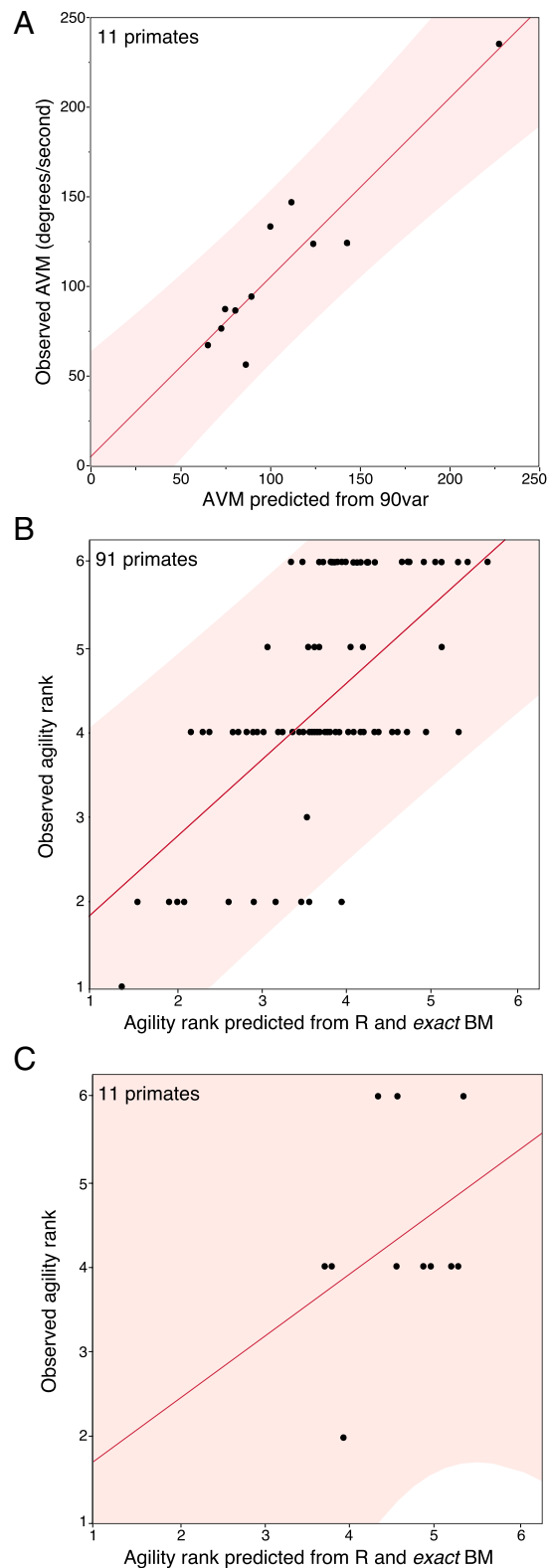
To examine the accuracy of Eq. 1, predicted AVM values were plotted against observed AVM for each species and confidence intervals were calculated (Fig. 3A). PGLS regressions were also used to generate equations predicting agility rank from body mass and  $R$  using either a published sample of 91 primates (2) or our sample of 11 strepsirrhines; the resulting observed versus predicted agility ranks are shown in Fig. 3B and C. Eq. 1 does not require information about body size and yields more accurate predictions than those achieved using body mass and  $R$  (confidence intervals of Fig. 3A vs. B and C).

### Discussion

We examined the relationship between locomotor head rotations and semicircular canal morphology in primates. Although our data do not support widely held assumptions that head rotations are functionally related to canal radius when body mass is accounted for, they point to an unexpected alternative: animals with fast head rotations have semicircular canals oriented more nearly at right angles to one another within each ear (i.e., they possess a low value of 90var).

Kinematic measurements of locomotor head movements exist for very few species, and even fewer have been acquired during naturalistic locomotion. Most previous studies have instead relied upon indirect proxies for head motion, such as agility ranks based on visual impressions of animal locomotion, with which to compare canal radius (2, 9, 31–36). Head rotations are the only relevant stimuli sensed by the semicircular canals, and so head rotations are the only measurable events physically linking canal morphology with locomotion. Because there was limited precedent for measuring locomotor head rotations, and because existing hypotheses did not specify which metrics of head rotation should be expected to correlate with canal morphologic variables, we performed an in-depth characterization of head rotations in a group of primates with varying locomotor repertoires and body size. We have established new canal metric variables that are highly correlated with head rotation and independent of body size. By establishing these functionally based correlates in a model group of strepsirrhine primates, this study will provide methods for future more generalized experimental studies of other species.

Prior work using much larger taxonomic samples has demonstrated a correlation between agility rank and the paired variables of body mass and  $R$  (2, 9). In the present study, AVM is not significantly correlated with either body mass ( $P = 0.090$ ) (Table S9),  $R$  ( $P = 0.227$ ) (Table S9), or both body mass and  $R$  together ( $P = 0.060$ ) (Eq. 3). It may be that our sample size was not large enough to detect a modest correlation among AVM, body mass, and  $R$ . It may also be that the agility rank variable used in previous studies and AVM are not measuring the same thing. Regardless, the unexpected and exciting finding is the very strong and body



**Fig. 3.** Accuracy of log-transformed morphological variables in predicting behavioral variables (95% confidence intervals shaded). (A) Observed versus predicted AVM calculated from 90var in 11 strepsirrhines (Eqs. 1 and 2). (B) Observed versus predicted agility rank from  $R$  and body mass (BM) in a sample of 91 primates, and (C) in our 11 strepsirrhines (data from Spoor et al. (2)). Because sample size influences confidence intervals, comparison of A with C better illustrates the relative strength of the underlying relationships between morphological and behavioral variables.

mass-independent correlation between 90var and AVM in our primate sample.

Eq. 1 offers a unique model for understanding canal functional morphology and for reconstructing animal movement. Although extant primates are most closely related to extinct ones, and therefore likely the most reliable models of extinct primate behavior, there are reasons to suspect that our results will be more broadly applicable to other vertebrate clades. First, the anatomy and physiology of the semicircular canal system is highly conserved; in testament to this fact, the method of vestibular sensitivity vector calculation used here has been used previously in studies of fish and rodents (14, 15). Second, as depicted in Fig. 2, 90var measurements from the nonprimate colugo and sloth are in accord with what would be predicted by Eq. 1, assuming that the seemingly fast-gliding colugo has a high AVM and the seemingly slow sloth has a low AVM. As described below, however, subjective impressions of animal speed or agility are not always predictive of AVM, and measurements of both 90var and AVM will be needed from other taxa to confirm the extent to which these results can be generalized to other clades.

As to why animals with high angular velocities might benefit from minimizing 90var, we suggest two possibilities. First, if the brain does not correct the vestibular signal gain for directional variation in sensitivity, then only rotations about axes of mean sensitivity would be interpreted with optimum accuracy (37). Second, the canals mechanically decompose head rotations into triaxial coordinates based on canal orientations (14). The brain must then perform coordinate transformations such that perceived rotation is resolved in the orthogonal coordinates of the animal's environment, and the efferent signals driving the vestibulo-ocular reflex are expressed in the nearly orthogonal arrangement of the extraocular muscles. It is therefore possible that data acquired by nearly orthogonal canals are processed more efficiently by the central nervous system. Conversely, it is difficult to imagine what advantage a high 90var value could confer to species with low angular velocities; we instead suggest that other functional and developmental demands on temporal bone shape take precedence over orthogonal canals in species with slow head rotations. Although we consider it unlikely, it is also possible that the correlation between 90var and AVM is not an adaptational relationship but instead reflects covariance of both 90var and AVM with a third unknown functional variable. Even if natural selection is shaping canal morphology to detect head rotations through one of the mechanisms suggested above, it is unknown whether low 90var is advantageous for successfully completing risky locomotor behaviors or for producing efficient movements during routine daily activity. That 90var is more highly correlated with AVM than with the mean of the fastest head rotations sampled from each behavior provides scant evidence in favor of the latter possibility. Studies dedicated to such questions will be needed to better characterize the relationship between 90var and rotational head speed.

Our results call into question several other commonly held assumptions in the literature. When considering an extinct species, the canal with the largest radius has been argued to lie roughly perpendicular to the axis of highest vestibular sensitivity. Based upon such estimates, canals with relatively large radius have been used to infer the speed of head rotation about individual axes in extinct dinosaurs, birds, and mammals, including humans, apes, and their extinct close relatives (3, 17, 38–43). The vector data presented here suggest that axes of high vestibular sensitivity do not align with axes of either fast or slow rotation in living animals. Our data fail to support reconstructions of axes of fast or slow rotation in extinct species based on which canal has the largest radius.

Existing inferences about agility in extinct species are based on a study of 210 extant mammals that were assigned agility ranks (rank 1 of “extra slow” through rank 6 of “fast”) based on visual

impressions (2). Multiple regressions comparing  $R$  versus the independent variables of body mass and agility rank yield a significant correlation ( $R^2 = 0.82$ ) (2, 37). However, body mass alone explains ~79% of the variation in  $R$ , whereas agility explains only 0.18% of the variation in  $R$  (37). Paleontologists have used  $R$  and body mass estimates to infer the agility of movement in extinct species (2, 4–10). Because  $R$  is so much more strongly correlated with body mass than with agility, such inferences can be considered reliable only when body mass is known precisely.

Our findings highlight the need to refine what aspects of locomotion might be revealed from semicircular canal measurements. The semicircular canal system detects only the angular movements of the head. Subjective impressions of “agility” used in prior studies are unlikely to have discriminated between the relevant angular components of head movement and the linear components of head movement, which go undetected by the semicircular canals. Additionally, the locomotor categories commonly used in behavioral studies (e.g., walking, running, leaping) tend to describe the activity of the postcranium, but the relationship between such locomotor categories and patterns of head rotation is not always intuitive. A field behaviorist might consider the quadrupedal *Microcebus* “slower” than the leaping *Propithecus* [the agility rank for the former was “medium” compared with “fast” for the latter in Spoor et al. (2)]. Although this difference might be true of the postcranial linear velocities of these two species, our data suggest that *Microcebus* generally exhibits slightly faster angular velocities of the head than *Propithecus* (the AVM for the former is 133°/s compared with 123°/s for the latter).

In addition to helping define the limits of canal-based locomotor reconstruction, our primate data may give rise to a more practical alternative means of inferring how extinct animals moved. Eq. 1 is based on 90var and is independent of body size (2, 7, 9). To measure 90var, just one set of three canals must be available, which is the same amount of fossil material that has been required to measure  $R$  in prior studies. Body mass estimates vary greatly for extinct taxa, especially for those species with fragmentary postcranial remains in which canal-based locomotor reconstructions would be most interesting, and the ability to predict behavior without knowing body mass will be a substantial advantage.

## Materials and Methods

**Kinematic Data Collection.** Eight study behaviors, as detailed in Table 1, were identified before kinematic data were collected. Subjects were presented with various supports to facilitate different study behaviors (Fig. S1). Terrestrial walking, terrestrial running, and bipedal leaping were performed on a level floor. Construction and use of arboreal and leaping supports is described in *SI Materials and Methods*. Kinematic data were collected from animals at the Duke Lemur Center under Duke University Institutional Animal Care and Use Committee protocol A081-07-03. Each subject was fitted with a cap bearing an array of reflective tracking markers. See *SI Materials and Methods* for details concerning marker placement, the camera array used to collect 3D kinematic data, and kinematic data processing (28, 44).

**Construction of Weighted AVM.** Angular velocity vector data were converted to scalar data to permit analysis by PGLS regression. Angular velocity magnitude was calculated from each three-component angular velocity vector. Single-behavior means were calculated from all angular velocity magnitudes sampled from individuals of a single species engaging in a single study behavior (Table S1, single-behavior means of angular velocity magnitude). Single-behavior means were used to construct a weighted AVM for each species.

To calculate AVM, behavioral weights were set up based on published locomotor budgets showing the percentage of time each species spends in locomotor modes that approximate our study behaviors. Four methods were developed to calculate behavioral weights (Table S4); the choice of method used to analyze each species depended upon the species' locomotor repertoire and the availability of published behavioral studies. See *SI Materials and Methods* for additional details.

**Morphologic Data Collection and Processing.** Morphologic measurements were made from CT scans of skulls and used to predict the sensitivity of the vestibular system to rotations in different directions. Osteologic specimens and associated CT scans are listed in [Table S2](#). CT scans were analyzed using Matlab (The Mathworks) ([Dataset S1](#)). Canal morphology was characterized by measuring the 3D locations of 90–200 points, or centroids, along the central streamline of each canal (16, 30). Centroid coordinates were scaled and rotated, by means of matrix transformation, into a standard position based on the Frankfort plane. Canal radius and canal orientation were determined by fitting a circle and a plane to all centroids, respectively. This process was repeated for all six canals in a specimen. These data were used to predict the vestibular sensitivity of the six-canal system to 64,800 axes of rotation spaced at 1° increments about the head (Fig. 1B) (14, 16). See [SI Materials and Methods](#) for details.

Angles among canal planes of best fit were determined by calculating the angles between pairs of positive orientation vectors for the six canals in each specimen (30). For each species, Rvar, 90var, and 180var were calculated as discussed in [Results \(Table S10\)](#). Published measurements were used for body mass ([Table S10](#)) (20).

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