Functional Implications of Ubiquitous Semicircular Canal Non-Orthogonality in Mammals

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Abstract

The ‘canonical model’ of semicircular canal orientation in mammals assumes that 1) the three ipsilateral canals of an inner ear exist in orthogonal planes (i.e., orthogonality), 2) corresponding left and right canal pairs have equivalent angles (i.e., angle symmetry), and 3) contralateral synergistic canals occupy parallel planes (i.e., coplanarity). However, descriptions of vestibular anatomy that quantify semicircular canal orientation in single species often diverge substantially from this model. Data for primates further suggest that semicircular canal orthogonality varies predictably with the angular head velocities encountered in locomotion. These observations raise the possibility that orthogonality, symmetry, and coplanarity are misleading descriptors of semicircular canal orientation in mammals, and that deviations from these norms could have significant functional consequences. Here we critically assess the canonical model of semicircular canal orientation using high-resolution X-ray computed tomography scans of 39 mammal species. We find that substantial deviations from orthogonality, angle symmetry, and coplanarity are the rule for the mammals in our comparative sample. Furthermore, the degree to which the semicircular canals of a given species deviate from orthogonality is negatively correlated with estimated vestibular sensitivity. We conclude that the available comparative morphometric data do not support the canonical model and that its overemphasis as a heuristic generalization obscures a large amount of functionally relevant variation in semicircular canal orientation between species.

Introduction

Detection of angular head accelerations is mediated by the semicircular canals of the inner ear. Each semicircular canal consists of a toroidal bony passage within the petrous portion of the temporal bone and contains an endolymph-filled duct. When the head rotates, inertial drag of endolymph within the duct acts upon sensory hair cells that modulate the firing rates of primary vestibular afferent neurons. Firing rates are either increased or decreased depending on the direction of head rotation [1]. The excitatory and inhibitory signals from all six semicircular canals are combined in the brain to generate reflexive movements that help to stabilize the eyes and head when the body is in motion [2].

In contrast with more readily accessible peripheral sense organs like the eye, the fact that the inner ear is encased within dense bone has hampered the comparative study of semicircular canal anatomy. This limitation, combined with the assumption that the three canals in each inner ear evolved to optimally detect rotations in each of the three orthogonal spatial dimensions, led researchers to rely on a series of simplifying assumptions about semicircular canal anatomy that are seldom critically examined. According to this “canonical model” of semicircular canal morphology, the plane of each canal is orthogonal to the planes of the other two ipsilateral canals so that all three canals in a single inner ear intersect at 90° angles [3–9]. Furthermore, contralateral semicircular canals are assumed to be essentially identical in dimension and orientation [4,10]. As a result, corresponding left and right canal pairs are expected to have equivalent angles and contralateral synergistic canals are expected to occupy parallel planes (Figure 1). These three basic components of the model, including orthogonality, angle symmetry, and coplanarity, are stated explicitly or implicitly in nearly every textbook or academic review covering the vestibular system [11–16]. Nonetheless, some empirical studies that measured semicircular canal orientation in a limited range of species reported results that are considerably divergent from the canonical model [e.g. 17,18–23]. Humans, for example, are reported to have ipsilateral canal pairs that differ by as much as 22° from orthogonality [17].

The comparative morphology of semicircular canals is important because canal orientation ostensibly influences vestibular function [24–26]. However, most comparative analyses have examined the relationship between semicircular canal radius of curvature and locomotor agility [27–31]. Although radius of curvature is a major determinant of the sensitivity in each canal, the orientations of all six canals also help determine the relative sensitivity of the vestibular system to angular accelerations in three dimensions [15,24–26,32].

As a result, some authors have incorporated canal orientation in their calculations of vestibular sensitivity to angular accelerations [25,33,34]. To date, the largest comparative analysis of
three-dimensional vestibular sensitivity focused on semicircular canal morphology and locomotor kinetics in 11 species of strepsirrhine primates [35]. This study found substantial variation between species in the homogeneity of three-dimensional sensitivity maps, and demonstrated that strepsirrhines with more orthogonal canals tend to encounter higher angular head velocities during locomotion. More broadly, this analysis also provided evidence that deviations from canal orthogonality have important consequences for vestibular function.

In contrast to early studies of vestibular anatomy that relied on gross dissection or histology (11, 12, 19, 22, 28–30), computed tomography is now the standard for studies of semicircular canal morphology because it is nondestructive, quantitative, and can provide excellent resolution of internal cranial spaces [36,37]. We used high-resolution x-ray computed tomography scans of bilateral inner ear labyrinths to quantify semicircular canal size and orientation in 39 extant species from 11 mammalian orders (Table 1). For each taxon in our sample, these data were used to quantify mean deviations of ipsilateral semicircular canal pairs from orthogonality (90var), the degree to which corresponding contralateral canal pair angles differ (Angle Symmetrydev), and the degree to which synergistic canal pairs deviate from coplanarity (Coplanaritydev). The term 90var was introduced by Malinzak et al. as the sum of the absolute value of the difference between each of three unilateral ipsilateral canal pair angle and 90° [35]. Here we calculate 90var by summing the absolute value of the difference between all six ipsilateral semicircular canal pair angles and 90°, and taking the mean (see below).

We also used bilateral measurements of the size and orientation of all six semicircular canals to estimate the maximum (Sensitivitymax) and average (Sensitivityave) sensitivity of the vestibular system to angular accelerations in three dimensions. These data for a large and taxonomically diverse sample allowed us to examine the degree to which orthogonality, symmetry, and coplanarity are characteristic of mammalian semicircular canals and to determine whether deviations from these norms are correlated with interspecific differences in estimated vestibular sensitivity.

Figure 1. Bony inner ear endocast of *Petauroides volans* (AMNH 150055) showing embedded head-centered reference planes and SCC canal pair types. A, dorsal view showing X, Y, and Z axes. Center point occurs at intersection of all three planes. Axial plane = YZ reference plane passing through the interaural line; frontal plane = XY reference plane defined by Reid’s Plane (perpendicular to viewer); sagittal plane = XZ reference plane passing through central features. B, Left lateral view with sagittal plane perpendicular to viewer. Abbreviations: A, ampulla; C, cochlea; CC, common crus; LASC, left anterior semicircular canal; LLSC, left lateral semicircular canal; LPSC, left posterior semicircular canal; R, arc radius of curvature of the left anterior semicircular canal; S, saccule; U, utricle. doi:10.1371/journal.pone.0079585.g001
The crania of 39 extant mammals, each representing a different genus, were scanned at the University of Texas High-Resolution X-ray Computed Tomography Facility (Austin, Texas). This facility maintains an archive of all scans used in this analysis. 

**Table 1.** Taxa, museum specimen number, High Resolution X-ray Computed Tomography image slices used for skull images, spacing between image slices in image stack, Field of Reconstruction, and image slice pixel size.

| Taxon                        | Common Name                     | Museum Specimen Number | Number of slices | Interslice Spacing (mm) | Field of Reconstruction (mm) | File size (pixels) |
|------------------------------|---------------------------------|------------------------|-----------------|-------------------------|------------------------------|-------------------|
| Acrobares pygmaeus           | Pygmy Gliding Possum            | AMNH 155057            | 406             | 0.03                    | 28.0                         | 1024 × 1024       |
| Allocata major               | Five-toed Jerboa                | AMNH 178795            | 1170            | 0.04                    | 37.0                         | 1024 × 1024       |
| Anomalurus beecrofti         | Scaly-tailed Flying Squirrel    | AMNH 50483             | 1270            | 0.04                    | 39.0                         | 1024 × 1024       |
| Caluromys sp.                | Woolly Opossum                  | AMNH 95526             | 746             | 0.08                    | 38.0                         | 1024 × 1024       |
| Cavia porcellus              | Guinea Pig                      | TMM M-7283             | 1524            | 0.04                    | 42.0                         | 1024 × 1024       |
| Cercartetus caudatus         | Dormouse Possum                  | AMNH 155090            | 705             | 0.04                    | 18.0                         | 1024 × 1024       |
| Chinchilla laniger           | Chinchilla                      | Hullar                 | 1887            | 0.04                    | 40                            | 1024 × 1024       |
| Chironectes minimus          | Water Opossum                    | AMNH 129701            | 1522            | 0.04                    | 33.0                         | 1024 × 1024       |
| Chrysocloris sp.             | Golden Mole                      | AMNH 82372             | 513             | 0.05                    | 31.0                         | 1024 × 1024       |
| Crocuta crocuta              | Hyena                            | UCMVZ 184551           | 528             | 0.50                    | 166.0                        | 512 × 512         |
| Dactylopsila trivirgata      | Striped Possum                   | AMNH 104040            | 1301            | 0.05                    | 45.0                         | 1024 × 1024       |
| Dolichotis patagonum         | Patagonian Hare                  | AMNH 80078             | 1705            | 0.07                    | 56.2                         | 1024 × 1024       |
| Dromiciops gliroides         | Monito del Monte                 | FMNH 127463            | 711             | 0.04                    | 16.6                         | 1024 × 1024       |
| Enhydra lutris               | Sea Otter                        | SO 2853-97             | 645             | 0.22                    | 106.0                        | 1024 × 1024       |
| Felis catus                  | Domestic Cat                     | TMM M-628              | 606             | 0.15                    | 70.0                         | 1024 × 1024       |
| Glaucomys volans             | Eastern Flying Squirrel          | TMM M-6332             | 474             | 0.08                    | 22.9                         | 522 × 522         |
| Hemibelideus lemuroides      | Brush-tipped Ring-tailed Possum  | AMNH 154375            | 1207            | 0.05                    | 40.0                         | 1024 × 1024       |
| Heteroccephalus glaber       | Naked Mole Rat                   | AMNH 113974            | 1050            | 0.02                    | 21.0                         | 1024 × 1024       |
| Lepus californicus           | Hare                             | TMM M-7500             | 660             | 0.14                    | 67.0                         | 1024 × 1024       |
| Meriones unguiculatus        | Gerbil                           | TMM M-05306            | 1394            | 0.02                    | 23.0                         | 1024 × 1024       |
| Monodelphis domestica        | Short-tailed Opossum             | TMM M-9039             | 885             | 0.14                    | 21.0                         | 1024 × 1024       |
| Mus musculus                 | House Mouse                      | TMM M-3196             | 737             | 0.03                    | 13.5                         | 1024 × 1024       |
| Notoryctes typhlops          | Marsupial Mole                    | AMNH 202107            | 705             | 0.04                    | 18.0                         | 1024 × 1024       |
| Ornithorynchus anatinus      | Duck-billed Platypus              | TMM M-5899             | 1998            | 0.05                    | 43.0                         | 1024 × 1024       |
| Pedetes capensis             | Springhare                       | AMNH 42016             | 1145            | 0.07                    | 67.0                         | 1024 × 1024       |
| Petauridae volans            | Greater Gliding Possum           | AMNH 150055            | 1251            | 0.05                    | 48.0                         | 1024 × 1024       |
| Petaurus breviceps           | Sugar Glider                     | TMM M-8226             | 555             | 0.07                    | 33.0                         | 1024 × 1024       |
| Petrophales dahlii           | Rock Possum                      | AMNH 183391            | 1424            | 0.05                    | 46.0                         | 1024 × 1024       |
| Potorous tridactylus         | Long-nosed Potoroo               | AMNH 65337             | 915             | 0.01                    | 48.0                         | 1024 × 1024       |
| Pseudocheirus peregrinus     | Common Ring-tailed Possum        | TMM M-847              | 795             | 0.09                    | 43.0                         | 1024 × 1024       |
| Pseudochoirus cupreus        | Coppery Ring-tailed Possum       | AMNH 151829            | 1289            | 0.05                    | 49.5                         | 1024 × 1024       |
| Pseudocharus forbesi         | New Guinean Ring-tailed Possum   | AMNH 104136            | 1339            | 0.03                    | 33.0                         | 1024 × 1024       |
| Rattus norvegicus            | Brown Rat                        | TMM M-2272             | 1571            | 0.03                    | 28.0                         | 1024 × 1024       |
| Saimiri sciureus             | Squirrel Monkey                  | NSm7                   | 310             | 0.07                    | 64.0                         | 1024 × 1024       |
| Sciurus niger                | Fox Squirrel                     | UMMZ 123729            | 450             | 0.16                    | 44.4                         | 512 × 512         |
| Talpa europaea               | Old World Mole                   | UCLGMZ 5437            | 585             | 0.06                    | 18.5                         | 1024 × 1024       |
| Tarsonipe rostratus          | Honey Possum                     | AMNH 119717            | 921             | 0.03                    | 13.0                         | 1024 × 1024       |
| Vulpes vulpes                | Red Fox                          | UCLA 13112             | 825             | 0.17                    | 80.0                         | 1024 × 1024       |
| Wallabia bicolor             | Swamp Wallaby                    | TMM M-4169             | 885             | 0.16                    | 74.5                         | 1024 × 1024       |

Museum Abbreviations: AMNH, American Museum of Natural History, New York; FMNH, Field Museum of Natural History, Chicago; TMM, Texas Natural Science Centers, Vertebrate Paleontology, Austin; UCL GMZ, University College, London Grant Museum of Zoology; SO, University of California Los Angeles Museum; UCLA, University of California Los Angeles; UCMVZ, University of California Museum of Vertebrate Zoology, Berkeley; UMMZ, University of Michigan Museum of Zoology, Ann Arbor.

doi:10.1371/journal.pone.0079585.t001

**Materials and Methods**

The crania of 39 extant mammals, each representing a different genus, were scanned at the University of Texas High-Resolution X-ray Computed Tomography Facility (Austin, Texas). This facility maintains an archive of all scans used in this analysis. Taxon, museum specimen number, and scan parameters for each cranium used in this study are listed in Table 1. With the
### Table 2. Summary of semicircular canal angle relationships.

| Taxon         | LASC $\alpha$ LLSC IPS | LASC $\alpha$ LPSC IPS | LLSC $\alpha$ LPSC IPS | RASC $\alpha$ RPSC IPS | RASC $\alpha$ RPSC IPS | RLSC $\alpha$ RPSC IPS | LASC $\beta$ RPSC SYN | LPSC $\beta$ RAS SYN | LLSC $\beta$ RLSC SYN |
|---------------|-------------------------|------------------------|------------------------|------------------------|------------------------|------------------------|-----------------------|----------------------|----------------------|
| Acrobates     | 103.86                  | 90.54                  | 81.01                  | 98.35                  | 89.17                  | 86.43                  | 7.63                  | 9.86                 | 8.95                 |
| Allactaga     | 72.26                   | 82.03                  | 86.86                  | 71.09                  | 83.50                  | 84.69                  | 19.58                 | 19.55                | 10.55                |
| Anomalurus    | 86.65                   | 104.52                 | 97.34                  | 88.10                  | 102.05                 | 97.77                  | 4.39                  | 7.52                 | 1.44                 |
| Caluromys     | 83.19                   | 96.48                  | 89.63                  | 77.14                  | 97.75                  | 87.54                  | 10.36                 | 10.03                | 26.72                |
| Cavia         | 82.29                   | 86.47                  | 85.12                  | 88.99                  | 87.10                  | 84.44                  | 7.11                  | 6.69                 | 1.19                 |
| Cercartetus   | 84.15                   | 91.73                  | 87.35                  | 81.53                  | 87.41                  | 84.80                  | 9.97                  | 7.99                 | 25.90                |
| Chinchilla    | 86.19                   | 84.87                  | 83.58                  | 74.51                  | 87.09                  | 81.58                  |                       |                      |                      |
| Chironectes   | 82.09                   | 104.33                 | 91.91                  | 77.84                  | 93.55                  | 91.69                  | 13.08                 | 11.69                | 20.25                |
| Chrysocloës   | 58.82                   | 86.41                  | 103.87                 | 71.65                  | 84.12                  | 81.58                  | 15.48                 | 10.06                | 14.71                |
| Crocuta       | 80.54                   | 95.71                  | 99.05                  | 81.39                  | 94.32                  | 90.01                  | 3.59                  | 8.48                 | 13.20                |
| Daicylopsila  | 82.82                   | 89.83                  | 94.77                  | 88.04                  | 95.08                  | 96.03                  | 9.25                  | 2.69                 | 7.16                 |
| Dolichotis    | 88.13                   | 89.25                  | 88.36                  | 74.61                  | 75.16                  | 89.79                  | 14.26                 | 1.58                 | 17.54                |
| Dromiciops    | 92.87                   | 89.71                  | 92.39                  | 88.75                  | 101.19                 | 94.69                  | 19.17                 | 14.68                | 15.27                |
| Erhydra       | 89.35                   | 98.42                  | 91.64                  | 91.16                  | 102.79                 | 83.18                  | 3.91                  | 0.51                 | 8.55                 |
| Felis         | 87.27                   | 83.62                  | 81.94                  | 83.79                  | 84.62                  | 81.65                  | 12.57                 | 11.53                | 10.75                |
| Glaucomys     | 86.71                   | 90.28                  | 94.48                  | 82.19                  | 87.17                  | 89.96                  | 5.66                  | 12.71                | 18.26                |
| Hemibelides   | 83.86                   | 105.74                 | 91.00                  | 78.14                  | 102.18                 | 85.44                  | 10.91                 | 9.13                 | 3.27                 |
| Heterocephalus| 79.61                   | 96.08                  | 96.45                  | 77.65                  | 90.61                  | 97.21                  | 10.84                 | 10.96                | 20.34                |
| Lepus         | 87.92                   | 93.87                  | 87.13                  | 87.87                  | 95.84                  | 87.45                  | 4.60                  | 5.19                 | 0.61                 |
| Meliones      | 88.92                   | 87.66                  | 82.46                  | 84.03                  | 89.03                  | 86.05                  | 1.66                  | 2.55                 | 4.49                 |
| Monodelphis   | 83.90                   | 95.59                  | 91.06                  | 81.31                  | 99.56                  | 89.32                  | 15.05                 | 17.04                | 24.19                |
| Mus           | 85.82                   | 78.08                  | 85.21                  | 85.84                  | 84.89                  | 85.26                  | 6.09                  | 10.45                | 9.91                 |
| Notoryctes    | 78.61                   | 121.21                 | 93.47                  | 68.23                  | 107.69                 | 82.78                  | 6.74                  | 9.29                 | 17.44                |
| Ornithoryctes | 82.12                   | 80.10                  | 82.98                  | 75.70                  | 82.23                  | 88.63                  | 4.56                  | 6.70                 | 21.67                |
| Pedetes       | 94.52                   | 93.63                  | 89.23                  | 91.36                  | 93.12                  | 89.25                  | 6.64                  | 2.63                 | 3.00                 |
| Petaroides    | 82.95                   | 98.23                  | 85.29                  | 79.67                  | 93.42                  | 86.31                  | 11.04                 | 15.03                | 22.29                |
| Petarurus     | 80.42                   | 89.18                  | 98.58                  | 86.01                  | 91.33                  | 102.68                 | 2.00                  | 4.85                 | 3.21                 |
| Petrosieudes  | 76.77                   | 89.07                  | 93.20                  | 89.48                  | 89.09                  | 90.86                  | 15.74                 | 14.14                | 3.61                 |
| Potorous      | 91.64                   | 88.35                  | 88.41                  | 94.76                  | 87.65                  | 88.32                  | 5.74                  | 4.63                 | 5.01                 |
| Pseudocheirus | 84.86                   | 93.67                  | 92.90                  | 84.10                  | 98.52                  | 90.41                  | 19.13                 | 24.15                | 6.42                 |
| Pseudochirops| 93.28                   | 83.83                  | 104.81                 | 87.93                  | 87.37                  | 85.92                  | 11.87                 | 15.29                | 9.53                 |
| Pseudochirus | 92.18                   | 104.50                 | 98.10                  | 89.71                  | 101.19                 | 103.14                 | 9.93                  | 2.32                 | 7.64                 |
| Rattus        | 88.64                   | 87.63                  | 79.72                  | 84.10                  | 87.33                  | 81.97                  | 11.65                 | 9.96                 | 8.22                 |
| Saimiri       | 85.97                   | 79.77                  | 89.55                  | 87.26                  | 76.24                  | 88.10                  | 7.97                  | 12.29                | 5.52                 |
| Sclerus       | 79.26                   | 86.88                  | 90.60                  | 84.04                  | 82.88                  | 91.93                  | 5.54                  | 1.71                 | 6.10                 |
Table 2. Cont.

| Taxon   | LASC | LLSC | IPS | LLSC | IPS | LASC | SYN | RLSC | IPS | RASC | IPS | RPSC | IPS | LLSC | IPS | RASC | IPS | SYN | RLSC | IPS |
|---------|------|------|-----|------|-----|------|-----|------|-----|------|-----|------|-----|------|-----|------|-----|-----|------|-----|
| Talpa   | 76.67| 74.48| 91.73| 5.47 | 7.09| 102.77| 12.97| 18.59| 11.22| 7.51 |
| Vulpes  | 97.36| 92.06| 92.37| 10.04| 4.21| 91.73 | 11.82| 18.59| 19.54| 5.52 |
| Petauroides volans | 87.46| 83.76| 97.34| 10.04| 4.21| 91.73 | 11.82| 18.59| 19.54| 5.52 |
| Wallabia| 85.39| 87.79| 87.79| 10.04| 4.21| 91.73 | 11.82| 18.59| 19.54| 5.52 |

Mean: 85.01, Standard Deviation: 7.40

Includes angles between all three pairs of ipsilateral for left and right sides, angles between left and right contralateral angle pairs, and angles between three synergistic canal pairs, all in degrees. IPS: ipsilateral canal pair angle, SYN: synergistic canal pair angle.

For the present study, canal angle comparisons required stable head-centered reference planes, especially for angle comparison of contralateral canals. Three reference planes were determined and segmented into the 3D digital images before any other analysis was undertaken. The terminology follows that of vestibular researchers [e.g., 22,24,26]. Approximately eight small reference segments along the median sutures of the skull images (e.g., nasals, nasion, bregma, and medial palatine sutures) were aligned in a best-fit plane to define the vertical sagittal (XZ) plane. Numerous previous authors assumed that the LSC represents the horizontal plane of a live animal's head orientation, thus the alternative designation of the canal as the horizontal semicircular canal [e.g., 26,38,39], but that also assumed that both the left and right lateral canals lie within the same horizontal plane. Because this assumption is not correct (see below), we used bilateral measurements of Reid's line (the line extending from the lower edge of the orbit to the center of the aperture of the external auditory canal [40] to define the horizontal/frontal plane (XY). The axial (YZ) plane contained the line connecting the two external auditory meatuses (interaural line) perpendicular to the frontal and sagittal reference planes. The positive X axis of the resultant head-centered reference system passed through the rostrum, the positive Y axis passed through the left meatus, and the positive Z axis passed dorsally through the skull. Such a coordinate system was fitted successfully to all specimens except a Thylacinus, which was discarded for phylogenetic purposes.

Images were thresholded in VGStudioMax based on the density of the petrosal using the VG Studio density averaging tool. The selected region of the bony labyrinth was subsequently outlined for each CT slice image in VG StudioMax and added together to produce segments representing endocasts of both bony labyrinths in each specimen. A resulting file of the reference planes and bony labyrinth endocasts for Petauroides volans is shown in Figure 1. For our determination of canal orientations with regard to the reference planes in VG StudioMax, we used a measurement tool to select an array of points (~60–100 per canal) representing the lumen centers of a canal from the end of the ampulla, around the canal and including the common crus. A circle circumference for each canal was calculated by a linear regression best-fit of the selected lumen points. The radius to the semicircular canal circumference (R, in mm) was recorded for use in sensitivity calculations. The fitpoints were imported into a VG StudioMax best-fit calculation to obtain the plane containing that semicircular canal [19], defined by coordinates of the unit normal axis perpendicular to that plane. A plane's normal line has no polarity, but each semicircular canal can be rotated in a direction that provides an increase in afferent neuron firing rate (excitatory direction) or it may be rotated in the opposite direction to produce a decrease in afferent neuron firing rate (inhibitory direction). To express this additional information, the normal line, serving as an axis of rotation, was polarized to give a vector (V) showing excitatory sensitivity direction according to the right-hand rule as an exception of Chinchilla, for which a preexisting scan was made available by Dr. Timothy Hullar, all cranial specimens used in this analysis were scanned with the permission of the museums listed in Table 1. All crania were scanned bilaterally, ensuring that both the right and left semicircular canals were scanned in situ. This bilateral scanning protocol allowed measurements of contralateral canal pairs, a parameter that is rarely measured. Bilateral scanning also permitted the calculation of the vestibular sensitivity of each specimen to head rotations in three dimensions. The resulting image stacks were imported into VGStudioMax® (Versions 1.2 and 2.0; Volume Graphics GmbH, 2004 and 2007) for 3D imaging and analysis.
Table 3. Summary data for the 39 mammalian species in the comparative sample.

|          | ASC x LSC IPS | ASC x PSC IPS | LSC x PSC IPS | ASC x PSC SYN | LSC x LSC SYN |
|----------|---------------|---------------|---------------|---------------|---------------|
| Arithmetic Mean | 84.49         | 91.87         | 90.32         | 9.52          | 11.22         |
| Arithmetic Standard Deviation | 7.33          | 8.14          | 5.91          | 5.19          | 7.51          |
| Mean Direction | 84.50         | 91.85         | 90.32         | 9.52          | 11.21         |
| Circular Standard Deviation | 4.80          | 5.32          | 3.87          | 3.40          | 4.88          |

IPS: ipsilateral canal pair angle, SYN: synergistic canal pair angle. All angles in degrees.

doi:10.1371/journal.pone.0079585.t003

described by Ezure and Graf [19] and utilized by Calabrese and Hullar [22]. Mathematical calculation of angles between all canals was performed in VGStudioMax, with corrections to ensure all angles are internal (in lateral direction of skull) [see 19,41]. Naming convention of the angles closely follows that of Spoor and Zonneveld [42]. For example, LASC x LLSC refers to the angle between the left anterior semicircular canal and the left lateral semicircular canal. All angles measured for each species are listed in Table 2, and summary data for ipsilateral canal angles and synergistic contralateral canals are provided in Table 3. The summary angular data in Table 3 includes both arithmetic means with standard deviations, as well as mean directions with circular standard deviations calculated by treating our data as vectors [13]. The arithmetic mean and mean direction for these data demonstrated negligible differences (i.e., ≤0.02°), while the circular standard deviation is less than the arithmetic standard deviation (Table 3). In all analyses, our angular measurements were quantified as the absolute value of the deviation from an expected value (either 90° or 180°; see below). Although these measurements are expressed in degrees, the data used in all analyses are scalar and do not require the use of circular statistics.

Orthogonality, Symmetry, and Coplanarity Calculations

We quantified semicircular canal orientation by comparing the deviations of canal pair angles from the expected normative values. Deviation from orthogonality (90 var) [35] was calculated by taking the absolute value of the difference between each canal pair angle and 90°, adding those difference for all six ipsilateral canal pairs, and dividing by six. Deviation from side to side semicircular canal angle symmetry (Angle Symmetry dev) was calculated as the absolute value of the difference between the left canal pair angle and the corresponding right canal pair angle. To quantify deviation from coplanarity (Coplanarity dev) we first subtracted the angle between each synergistic contralateral canal pair from 180°. We then summed the absolute value of this difference for each of the three synergistic canal pairs and divided by 3. Values for these variables are given in Table 4.

Sensitivity Calculations

A rotation of the head in the plane of a given semicircular canal (i.e., around V) increases the firing rate of the vestibular nerve cells in that canal above a resting rate (in spikes · sec⁻¹), or decreases the firing rate (axis opposite to V). The rate of nerve cell firing change is proportional to R and the speed of rotation (in degrees · sec⁻¹), and is referred to as the sensitivity of the canal to rotation (in spikes · sec⁻¹/degrees · sec⁻¹) [16,24,25,32]. A head rotation around an axis with orientation X changes the sensitivity of the canal nerve responses in proportion to the cosine of the angle between X and V. The responses of all six individual semicircular canals to rotation along X can be determined with R and V for each canal, and the orientation of X. Therefore, for a head rotation along any head-centered axis X, the sensitivities of all six canals can be summed to provide a global sensitivity to the rotation (S, in spikes · sec⁻¹/degrees · sec⁻¹). By calculating such global sensitivities for a high number of rotational axes, an axis of rotation resulting in the maximum summed sensitivity of all six canals can be determined (Sensitivity max). The average sensitivity for a high number of rotational axes can also be calculated (Sensitivity ave). The Sensitivity max and Sensitivity ave values calculated for specimens used in this study are listed in Table 4. Both sensitivity values were calculated using Bubbles.mat [35] software, which is described in detail by Yang and Hullar [25], Rodgers [32], and Malinzak et al. [32]. Bubbles.mat uses both the orientation and radius of curvature of the six semicircular canals to calculate estimated sensitivity of the vestibular system to angular accelerations in three dimensions. According to the Bubbles.mat results, the calculated Sensitivity max is a function of both canal orientations and canal radii but Sensitivity ave is entirely determined by canal radii. These effects are illustrated in Figure 2, which shows the relationship between 90 var and the ratio of our observed sensitivities to sensitivity calculated with canals constrained to strict orthogonality (O Sensitivity max and O Sensitivity min) through setting all ipsilateral canal angles as 90° bilaterally, and setting ASC and PSC 45° away from the sagittal plane for Bubbles.mat calculations. In Figure 2, the ratio of Sensitivity ave to O Sensitivity ave is always 1.0 across a range of 90 var values which indicates that Sensitivity ave is solely a function of R. By comparison, the ratio of Sensitivity max to O Sensitivity max is always greater than 1.0 and tends to increase with increases in 90 var (Figure 2). This ratio of Sensitivity max : O Sensitivity max reflects the fact that artificially constraining strict orthogonality leads to a decrease in the maximum estimated sensitivity of the vestibular system according to the Bubbles.mat calculations. The implications of these effects for our analyses of canal orientation an estimated sensitivity are discussed below.

Statistical Analysis

All statistical tests were performed in R using the ape and nlme packages [44–46]. A normal distribution for all continuous data was confirmed using Shapiro-Wilk tests for normality. Raw data for 90 var and Angle Symmetry dev deviated significantly from normality, so these data were log10 transformed to satisfy the assumptions of parametric statistical tests. A normal distribution for both 90 var and Angle Symmetry dev following log10 transformation was confirmed with a Shapiro-Wilk test. Data for Coplanarity dev, Sensitivity max and Sensitivity ave did not deviate significantly from normality and were therefore included in analyses without transformation.

Two types of statistical tests were used assess the relationship between the morphology and estimated sensitivity of the semicircular canals. First, Pearson product-moment correlations were calculated for our three measures of canal morphology (90 var,
Angle Symmetry$_{dev}$ and Coplanarity$_{dev}$) and our two estimates of sensitivity to angular accelerations in three dimensions (Sensitivity$_{max}$ and Sensitivity$_{ave}$). (Table 5). Because we expect deviations from orthogonality (i.e., greater $90_{var}$ values), deviations from equality in corresponding contralateral angle pairs (i.e., greater Angle Symmetry$_{dev}$ values), and deviations from coplanarity in synergistic canal pairs (i.e., greater Coplanarity$_{dev}$ values) to be negatively correlated with vestibular sensitivity, all correlations were one-tailed. Second, phylogenetic generalized least-squares regression (PGLS) [47] was used to examine the relationships between canal morphology and estimated sensitivity while controlling for phylogenetic relationships. Tree topology and branch lengths for the included taxa follow Bininda-Emonds et al. [48,49].

Table 4. Deviations from orthogonality ($90_{var}$), side-to-side angle symmetry (Angle Symmetry$_{dev}$), and synergistic canal coplanarity (Coplanarity$_{dev}$).

| Taxon      | $90_{var}$ | Angle Symmetry$_{dev}$ | Coplanarity$_{dev}$ | $S_{max}$ | $S_{ave}$ | OS$_{max}$ | OS$_{ave}$ |
|------------|------------|------------------------|---------------------|-----------|-----------|------------|------------|
| Acrobates  | 6.02       | 4.10                   | 8.83                | 0.42      | 0.34      | 0.39       | 0.34       |
| Allocotaga | 9.93       | 1.60                   | 16.56               | 1.35      | 1.05      | 1.22       | 1.05       |
| Anomalurus | 7.82       | 1.45                   | 4.44                | 1.23      | 0.99      | 1.14       | 0.99       |
| Caluromys  | 6.12       | 3.13                   | 15.70               | 0.68      | 0.56      | 0.65       | 0.56       |
| Cavia      | 4.27       | 2.67                   | 5.00                | 1.17      | 0.97      | 1.12       | 0.97       |
| Cercartetus| 4.42       | 3.16                   | 14.32               | 0.49      | 0.34      | 0.40       | 0.34       |
| Chinchilla | 7.03       | 5.30                   | 1.39                | 1.10      | 1.27      | 1.1        |            |
| Chironectes| 7.20       | 5.49                   | 17.01               | 0.71      | 0.59      | 0.68       | 0.59       |
| Chrysochilis| 12.41     | 9.13                   | 13.41               | 0.38      | 0.27      | 0.32       | 0.27       |
| Crocuta     | 6.20       | 3.76                   | 8.41                | 2.17      | 1.78      | 2.07       | 1.78       |
| Dactylopsila| 4.20       | 3.91                   | 6.40                | 0.87      | 0.72      | 0.84       | 0.72       |
| Dolichotis  | 5.78       | 9.68                   | 11.13               | 1.62      | 1.30      | 1.50       | 1.3        |
| Dromiciops  | 3.78       | 5.97                   | 16.53               | 0.38      | 0.32      | 0.37       | 0.32       |
| Enhydra     | 5.25       | 4.88                   | 4.36                | 1.62      | 1.30      | 1.50       | 1.3        |
| Felis       | 6.19       | 1.59                   | 11.62               | 1.42      | 1.07      | 1.24       | 1.07       |
| Glaucomys   | 3.12       | 4.05                   | 12.21               | 0.88      | 0.74      | 0.85       | 0.74       |
| Hemibeleus  | 8.58       | 4.95                   | 7.79                | 1.52      | 1.17      | 1.37       | 1.17       |
| Heterocephalus| 7.18      | 2.73                   | 14.04               | 0.41      | 0.33      | 0.39       | 0.33       |
| Lepus       | 3.22       | 0.78                   | 3.48                | 1.35      | 1.13      | 1.31       | 1.13       |
| Meriones    | 3.64       | 3.28                   | 2.90                | 0.83      | 0.68      | 0.78       | 0.68       |
| Monodelphis | 5.35       | 2.64                   | 18.76               | 0.46      | 0.37      | 0.44       | 0.37       |
| Mus         | 5.82       | 2.29                   | 8.82                | 0.26      | 0.21      | 0.25       | 0.21       |
| Notoryctes  | 15.45      | 11.55                  | 11.14               | 0.38      | 0.27      | 0.32       | 0.27       |
| Ornithorhynchus| 8.04     | 4.73                   | 10.98               | 1.12      | 0.90      | 1.05       | 0.9        |
| Pedetes     | 2.36       | 1.23                   | 4.05                | 1.58      | 1.32      | 1.53       | 1.32       |
| Petauroides | 6.24       | 3.04                   | 16.12               | 1.11      | 0.92      | 1.07       | 0.92       |
| Petaurus    | 6.16       | 3.95                   | 3.39                | 0.73      | 0.58      | 0.67       | 0.58       |
| Petropseudes| 3.27       | 5.02                   | 11.16               | 1.16      | 0.93      | 1.08       | 0.93       |
| Potorous    | 2.28       | 1.31                   | 5.11                | 1.20      | 0.99      | 1.15       | 0.99       |
| Pseudocheirus| 4.42      | 2.70                   | 16.57               | 1.16      | 0.95      | 1.11       | 0.95       |
| Pseudochirops| 5.51      | 9.26                   | 12.23               | 1.11      | 0.92      | 1.07       | 0.92       |
| Pseudochirulus| 8.24      | 3.61                   | 6.63                | 1.00      | 0.79      | 0.92       | 0.79       |
| Rattus      | 5.10       | 2.36                   | 9.94                | 0.75      | 0.63      | 0.73       | 0.63       |
| Saimiri     | 5.52       | 2.09                   | 10.13               | 1.32      | 1.05      | 1.21       | 1.05       |
| Sciuromys   | 4.91       | 3.37                   | 4.47                | 1.65      | 1.32      | 1.53       | 1.32       |
| Talpa       | 8.78       | 8.73                   | 7.57                | 0.59      | 0.48      | 0.56       | 0.48       |
| Tarsipes    | 7.41       | 8.86                   | 8.15                | 0.26      | 0.20      | 0.23       | 0.2        |
| Vulpes      | 5.32       | 4.74                   | 8.72                | 1.62      | 1.30      | 1.51       | 1.3        |
| Wallabia    | 2.41       | 3.47                   | 16.66               | 1.81      | 1.55      | 1.81       | 1.55       |

Sensitivities calculated from canal dimensions [32] and angles from Table 2. Hypothetical ‘Orthogonal Sensitivity’ calculated by forcing all canal angles to be orthogonal and symmetrical, but keeping all R dimensions as originally measured.

doi:10.1371/journal.pone.0079585.t004
in each PGLS analysis was quantified using Pagel’s lambda ($\lambda$) [50].

**Results**

**Deviations from orthogonality, angle symmetry, and coplanarity**

We find that the angle between two ipsilateral canals ranges between 58.8° and 121.2° for the species in our sample (Table 2; Figure 3). The smallest canal pair angle in our sample (LASC\_LLSC in Chrysochloris) is 31.2° less than 90°, while the largest canal pair angle in our sample (LASC\_LPSC in Notoryctes) is 31.2° greater than 90°. The mean angle for all ipsilateral canal pairs across all taxa is 88.9° (st. dev. = 7.8°) and the average deviation from orthogonality for all ipsilateral canal pairs is 6.0° (st. dev. = 5.1°). Similarly, 90\_var ranges from a low value of 2.3° in Potorous to a high value of 15.5° in Notoryctes (mean = 6.0°, st. dev. = 2.6°). Of the ipsilateral canal pairs, ASC\_LSC is smallest, with a mean angle of 84.5° (st. dev. = 7.3°) and a 95% mean confidence interval of 83°–86° (i.e., excluding orthogonality). By comparison, mean ASC\_PSC is 91.9° (st. dev. = 8.1°) and mean LSC\_PSC is 90.3° (st. dev. = 5.9°) (Table 3).

In addition to these deviations from orthogonality, our data demonstrate that ipsilateral canal pair angles differ by an average of 4.3° (st. dev. = 2.6°) between the right and left sides of individual specimens. Mean Angle Symmetry\_dev values range from a low of 0.8° in Lepus to a high of 11.6° in Notoryctes. Angles between synergistic canal pairs range from 0.5° (Enhydra LPSC \_RASC) to 27.7° (Caluromys LLSC \_RLSC). The mean deviation from coplanarity is 9.5° (st. dev. = 5.2°) for the two ASC\_PSC pairs and 11.2° (st. dev. = 7.5°) for the LSC\_LSC pair (Table 3). The mean deviation of all three synergistic canal pair angles from coplanarity is 10.1° (st. dev. = 6.1°).

**Canal orientation and vestibular sensitivity**

As expected, there is a negative correlation between the two estimates of vestibular sensitivity and the three measures of semicircular canal orientation (Table 5). This relationship is significant at $P<0.05$ for all comparisons except that of Angle Symmetry\_dev and Sensitivity\_max, which are negatively correlated at $P=0.054$. These data demonstrate that species with lower

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**Table 5. Results of Statistical Tests.**

|                | 90\_var | Angle Symmetry\_dev | Coplanarity\_dev |
|----------------|---------|---------------------|------------------|
|                | Pearson: $P = 0.019^*$; $r = -0.333$ | Pearson: $P = 0.047^*$; $r = -0.272$ | Pearson: $P = 0.041^*$; $r = -0.286$ |
|                | PGLS: $P = 0.029^*$; $\lambda = 0.648$ | PGLS: $P = 0.236$; $\lambda = 0.636$ | PGLS: $P = 0.363$; $\lambda = 0.762$ |
| $S_{\text{ave}}$ | Pearson: $P = 0.036^*$; $r = -0.292$ | Pearson: $P = 0.054^*$; $r = -0.262$ | Pearson: $P = 0.046^*$; $r = -0.276$ |
|                | PGLS: $P = 0.060$; $\lambda = 0.682$ | PGLS: $P = 0.273$; $\lambda = 0.684$ | PGLS: $P = 0.372$; $\lambda = 0.791$ |

P-values for significant results and non-significant trends shown in bold; Results significant at $P<0.05$ marked with an asterisk. "Pearson" = one-tailed Pearson product-moment correlation, "PGLS" = phylogenetic generalized least-squares regression.
estimated sensitivity to angular accelerations tend to have semicircular canals that deviate more from orthogonality, angle symmetry, and coplanarity. However, the strength of these negative correlations is relatively modest, with correlation coefficients ranging between \(-0.262\) and \(-0.333\) (Table 5). Furthermore, when these relationships are analyzed using PGLS regression to control for phylogenetic non-independence, the results for Angle Symmetry\(_{\text{dev}}\) and Coplanarity\(_{\text{dev}}\) are non-significant. By contrast, the PGLS regression of 90\(_{\text{var}}\) and Sensitivity\(_{\text{ave}}\) remains significant at \(P = 0.029\) (Figure 4) and the PGLS regression of 90\(_{\text{var}}\) and Sensitivity\(_{\text{max}}\) is near significance at \(P = 0.060\). Lambda values for all six comparisons demonstrate that the relationships between these variables do not follow a strict Brownian motion model of evolution, nor are they completely free of the influence of phylogeny (Table 5). According to these results, phylogenetic proximity has the smallest influence on the relationship between Angle Symmetry\(_{\text{dev}}\) and vestibular sensitivity (\(\lambda \approx 0.64–0.68\)) and the greatest influence on the relationship between Coplanarity\(_{\text{dev}}\) and vestibular sensitivity (\(\lambda \approx 0.76–0.79\)).

**Discussion**

Our results reveal that the canonical model of semicircular canal orientation is not strictly correct for a wide range of mammalian species. In our comparative sample, angles between pairs of ipsilateral semicircular canals deviate from orthogonality by an average of \(6.0^\circ\), corresponding left-right canal pair angles differ by an average of \(4.3^\circ\), and synergistic canals deviate from coplanarity by an average of \(10.1^\circ\). Although the angle between any two ipsilateral semicircular canals does approach \(90^\circ\) when data are averaged for all canal pairs across all taxa, it is nevertheless clear that all mammals deviate from canal orthogonality to some degree. For example, *Potorous*, *Pedetes*, and *Wallabia* all have ipsilateral canal pair angles that diverge from \(90^\circ\) by an average of between only \(2^\circ\) and \(3^\circ\). By contrast, *Notoryctes*, *Chrysochloris*, and *Allactaga* all have ipsilateral canal pair angles that diverge from \(90^\circ\) by an average of nearly \(10^\circ\) or more. These data further underscore the fact that none of the taxa considered in this analysis has truly orthogonal semicircular canals, and that substantial deviations from orthogonality, symmetry, and coplanarity appear to be a common feature of vestibular anatomy in mammals. However, it is also important to acknowledge that our comparative sample does not address questions related to intraspecific variation in canal orientation, so it is currently unclear how representative the values reported here are for each species in our dataset (Tables 1, 2). Our results also demonstrate that the mean angle between the anterior and lateral canals is considerably less than \(90^\circ\) and is \(6.4^\circ–7.4^\circ\) lower than the mean angle between the other two ipsilateral canal pairs. In a functional
context, is not presently clear why the angle between ipsilateral anterior and lateral canals is systematically lower than that for other ipsilateral canal pairs, but this finding further reinforces the inaccuracy of general characterizations of semicircular canals as orthogonal [3–16].

Previously published studies of semicircular canal morphology in 43 living and fossil species support our general finding that substantial deviations from the canonical model are the norm for mammals (Table 6). When unilateral measurements are considered, these analyses document a range of ipsilateral canal pair angles between 52.2° and 117.0° and an average 90 var for all ipsilateral canal pairs of 7.9° (st. dev. = 4.4°). As in the species we examined, the published data also show that across taxa the angle between the anterior and lateral canals (ASC LSC mean = 82.6°, st. dev. = 11.3°) is considerably smaller than the angle between the other two ipsilateral canal pairs (ASC PSC mean = 93.6°, st. dev. 9.7°; LSC PSC mean = 91.4°, st. dev. = 7.4°). The published taxa also show a mean deviation from coplanarity of 16.9° (st. dev. = 6.7°) for both ASC PSC pairs and 13.3° (st. dev. = 6.9°) for the LSC LSC pair. The mean deviation of all three synergistic canal pair angles from coplanarity is 13.8° (st. dev. = 6.9°).

From a practical standpoint, these data have important implications for the use of lateral canal orientation as an indicator of the horizontal plane in reconstructions of head posture in fossil mammals [31,39,51–53]. In our comparative sample, 7 of the 39 species have right and left lateral canals that deviate from coplanarity by more than 20° (Table 2). This large amount of bilateral variation in lateral canal orientation within individual specimens suggests that the lateral canal is an imprecise indicator of habitual head orientation (resting or active) in fossil species, particularly if reconstructions are based on unilateral measurements of semicircular canals [54].

Our data also generally confirm the expectation that there are important functional consequences of the degree to which a species’ vestibular anatomy deviates from the canonical model. In particular, deviations from canal orthogonality (as measured by 90 var) are negatively correlated with both of our estimates of vestibular sensitivity (Table 5). This result is most pronounced for the relationship between 90 var and mean sensitivity (Sensitivity ave, Figure 4). As noted previously, the values for Sensitivity ave reported here are determined entirely by canal radii of curvature (Figure 2), so the significant negative relationship between 90 var and Sensitivity ave is unrelated to our methods for estimating canal sensitivity. By the same token, deviations from orthogonality tend to increase the maximum vestibular sensitivity (i.e., result in higher Sensitivity max: OSensitivity max ratio; Figure 2) according to the methods employed here. In other words, based on our estimates of canal sensitivity, constraining canals to be perfectly orthogonal always decreases Sensitivity max (Figure 2, Table 4). Accordingly, our results for 90 var and Sensitivity max (Table 5) should be interpreted with caution because estimated maximum vestibular sensitivity is determined both by the radii and orientations of canals. Nevertheless, our analysis demonstrates that as the average deviation from canal orthogonality in our interspecific comparative sample increases (i.e., higher 90 var), the mean estimated sensitivity to angular head accelerations tends to decrease. As a result, species with more orthogonal semicircular canals tend to have higher mean vestibular sensitivity than species with less orthogonal semicircular canals (Figure 4). Although canal radius of curvature remains a major determinant of semicircular canal sensitivity, these findings imply that selection for greater sensitivity

Figure 4. Regressions of mean estimated semicircular canal sensitivity (Sensitivity ave) on Log10 90 var.

doi:10.1371/journal.pone.0079585.g004

Semicircular Canal Orientation in Mammals
Table 6. Previous semicircular canal pair angle research results.

| Taxon                  | LASC (°) | LLSC (°) | LPSC (°) | RASC (°) | RLSC (°) | LASC (°) | LPSC (°) | RASC (°) | RLSC (°) | LASC (°) | LPSC (°) | RASC (°) | RLSC (°) | n | Sources and Notes |
|-----------------------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----------|----|------------------|
| Atelerix albiventris  | 82.20    | 91.70    | 92.10    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Balaenopteridae†      | 71.60    | 105.00   | 75.60    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Bathygenys Reeves†    | 86.00    | 99.60    | 91.30    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Canis familiaris      | 80.40    | 101.00   | 89.10    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Cavia porcellus       | 57.85    | 76.71    | 82.36    | 57.85    | 76.71    | 82.36    | 32.17    | 36.16    | 30.82    |          |          |          |          | 10 | Curthoys et al (1975)[1]a |
|                       | 6.13     | 5.49     | 4.74     | 6.13     | 5.49     | 4.74     | 4.42     | 4.86     | 10.05    |          |          |          |          |    |                   |
| Cavia porcellus       | 91.22    | 91.20    | 85.88    |          |          |          |          |          |          |          |          |          |          | 8  | Cox and Jeffery (2008) [2a] |
|                       | 7.64     | 6.34     | 6.17     |          |          |          |          |          |          |          |          |          |          |    |                   |
| Chinchilla            | 76.30    | 90.90    | 103.00   | 78.70    | 91.00    | 101.00   | 15.60    | 14.80    | 14.60    |          |          |          |          | 3  | Hullar and Williams (2006)*a |
| Isanegra              | ±2.7     | ±1.7     | ±5.7     | ±2.3     | ±6.9     | ±1.3     | ±0.3     | ±12      |          |          |          |          |          |    |                   |
| Chrysoclorhis sp.     | 65.60    | 86.90    | 96.70    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Cynocephalus valans   | 92.20    | 90.00    | 91.80    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Dasypus novemcinctus  | 62.40    | 67.70    | 87.30    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Didelphis virginiana  | 109.00   | 102.00   | 104.00   |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Elephas†              | 66.30    | 73.70    | 96.70    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Equus caballus        | 84.70    | 93.30    | 90.10    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Eumetopius jubatus    | 79.70    | 105.00   | 90.60    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Felis catus           | 95.60    | 87.90    | 94.10    | 95.60    | 87.90    | 94.10    | 81.10    | 13.90    | 13.90    | 14.40    |          |          |          | 3  | Ezure & Graf (1984) [1a] |
| Felis catus           | 89.62    | 90.21    | 94.23    | 89.62    | 90.21    | 94.23    | 13.92    | 14.49    | 12.49    |          |          |          |          | 7  | Blanks et al. (1972) [1a] |
|                       | ±8.71    | ±4.05    | ±3.84    | ±8.71    | ±4.05    | ±3.84    | ±3.99    | ±4.52    | ±9.21    |          |          |          |          |    |                   |
| Felis catus           | 9.72     | 4.49     | 4.08     | 9.72     | 4.49     | 4.08     | 28.66    | 31.19    | 73.74    |          |          |          |          |    |                   |
|                       | 78.36    | 103.34   | 89.49    |          |          |          |          |          |          |          |          |          |          | 8  | Cox and Jeffery (2008) [2a] |
| Felis catus           | ±10.05   | ±9.7     | ±6.94    |          |          |          |          |          |          |          |          |          |          |    |                   |
|                       | 12.83    | 9.39     | 7.76     |          |          |          |          |          |          |          |          |          |          |    |                   |
| Felis catus           | 76.80    | 91.40    | 96.70    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Hemicentetes semispinosus | 85.40  | 117.00   | 92.60    |          |          |          |          |          |          |          |          |          |          | 1  | Ekdale (2009) [3]c |
| Homo sapiens          | 90.60    | 94.40    | 90.40    | 90.60    | 94.40    | 90.40    | 103.40   | 15.30    | 15.30    | 11.30    |          |          |          | 10 | Della |

Sources and Notes:
- [1] Curthoys et al (1975)*
- [2] Cox and Jeffery (2008)
- [3] Ekdale (2009)
| Taxon                        | LASC  | LASC  | LLSC  | LASC  | RASC  | RASC  | RLSC  | LASC  | LASC  | LPSC  | LASC  | RASC  | RASC  | LLSC  | LPSC  | LASC  | RASC  | LPSC  | LLSC  | n  | Sources and Notes |
|-----------------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|     |                          |
| Homo sapiens               | 68.24 | 86.16 | 95.75 | 68.24 | 86.16 | 95.75 | 24.56 | 23.73 | 19.82 | 10    | Blanks et al. (1975)* [1]a |
|                            | ±7.55 | ±4.72 | ±4.66 | ±7.55 | ±4.72 | ±4.66 | ±7.19 | ±6.77 | ±14.93 | 7     | Hashimoto et al. 2005a   |
|                            | 11.06 | 5.48  | 4.87  | 11.06 | 5.48  | 4.87  | 29.28 | 28.28 | 75.33 |                   |
| Homo sapiens               | 90.50 | 91.70 | 94.62 | 90.50 | 91.70 | 94.62 | 10    | 9.71  | 7.2   |       |                    |
|                            | ±2.98 | ±1.85 | ±3.32 | ±2.98 | ±1.85 | ±3.32 | ±3.32 |       |       |                   |
|                            | 3.29  | 2.02  | 3.51  | 3.29  | 2.02  | 3.51  |       |       |       |                   |
| Homo sapiens               | 85.30 | 97.14 | 88.96 | ±5.81 | ±4.82 | ±6.33 | 6.81  | 4.96  | 7.12  | 6     | Jeffery (2008) [2]a       |
|                            |       |       |       |       |       |       |       |       |       |                   |
| Homo sapiens               | 98.90 | 100.00| 89.80 | 68.24 | 86.16 | 95.75 | 24.56 | 23.73 | 19.82 | 10    | Blanks et al. (1975)* [1]a |
| Kulbeckia kulbecki         | 79.90 | 79.90 | 89.60 | 68.24 | 86.16 | 95.75 | 24.56 | 23.73 | 19.82 | 10    | Blanks et al. 2005a       |
| Lepus californicus         | 84.20 | 94.00 | 88.60 | 68.24 | 86.16 | 95.75 | 24.56 | 23.73 | 19.82 | 10    | Blanks et al. 2005a       |
| Macaca mulatta             | 98.73 | 86.48 | 88.49 | 98.73 | 86.48 | 88.49 | 10    | 11.18 | 2.24  | 10    | Blanks et al. 2005a       |
|                            | ±5.39 | ±3.43 | ±3.91 | ±5.39 | ±3.43 | ±3.91 | ±3.32 | ±3.12 | ±0.77 |
|                            | 5.46  | 3.97  | 4.42  | 5.46  | 3.97  | 4.42  | 33.27 | 27.91 | 34.38 |
| Macaca mulatta             | 83.10 | 100.00| 89.00 | 68.24 | 86.16 | 95.75 | 24.56 | 23.73 | 19.82 | 10    | Blanks et al. 2005a       |
| Macroscelides proboscideus | 100.00| 90.70 | 73.50 | 68.24 | 86.16 | 95.75 | 24.56 | 23.73 | 19.82 | 10    | Blanks et al. 2005a       |
| Manis tricuspid             | 77.00 | 84.80 | 88.60 | 68.24 | 86.16 | 95.75 | 24.56 | 23.73 | 19.82 | 10    | Blanks et al. 2005a       |
| Mus C57BL/6J               | 92.56 | 99.02 | 101.17| 91.55 | 99.26 | 101.26| 17.61 | 17.66 | 9.14  | 4     | Calabrese and Hullar (2006)a |
|                            | ±1.93 | ±1.46 | ±0.97 | ±1.02 | ±1.29 | ±0.96 | ±2.73 | ±1.43 | ±0.98 |
|                            | 2.09  | 1.47  | 0.96  | 1.11  | 1.30  | 0.95  | 15.50 | 8.10  | 10.72 |
| Mus CBA/Cal                | 96.82 | 89.65 | 102.29| 95.47 | 88.94 | 102.05| 11.00 | 14.79 | 10.42 | 4     | Calabrese and Hullar (2006)a |
|                            | ±5.73 | ±2.51 | ±1.86 | ±1.94 | ±1.98 | ±2.14 | ±1.24 | ±2.11 | ±3.8  |
|                            | 5.92  | 2.80  | 1.82  | 2.03  | 2.23  | 2.10  | 11.27 | 14.27 | 36.47 |
| Mus musculus               | 76.63 | 101.54| 96.08 | 68.24 | 86.16 | 95.75 | 24.56 | 23.73 | 19.82 | 10    | Blanks et al. 2005a       |
|                            | ±6.02 | ±6.32 | ±6.06 | 7.86  | 6.22  | 6.31  |       |       |       |                   |
| Mus musculus               | 88.80 | 94.40 | 95.60 | 68.24 | 86.16 | 95.75 | 24.56 | 23.73 | 19.82 | 10    | Blanks et al. 2005a       |
| Nycticebus coucang         | 85.90 | 112.00| 94.90 | 68.24 | 86.16 | 95.75 | 24.56 | 23.73 | 19.82 | 10    | Blanks et al. 2005a       |
| Nycticebus coucang         | 88.60 | 88.60 | 68.20 | 114.40| 23.10 | 23.10 | 61.06 |       |       | 3     | Matano et al. (1985) [1]c  |

Table 6. Cont.
Table 6. Cont.

| Taxon                      | LASC | LLSC | IPS | RASC | RASC | RLSC | LASC | LPSC | LASC | LPSC | IPS | RASC | RASC | RLSC | LPSC | IPS | Sources and Notes |
|----------------------------|------|------|-----|------|------|------|------|------|------|------|-----|------|------|------|------|-----|-------------------|
| Orycteropus afer           | 78.50| 91.90| 95.70|      |      |      |      |      |      |      |     |      |      |      |      |     | Ekdale (2009) [3]c |
| Oryctolagus cuniculus      | 79.80| 76.60| 75.50| 79.80| 76.60| 75.50| 90.50| 116.50| 13.60| 13.60| 8.60|      |      |      |      |     | Ezure & Graf (1984) [1a] |
| Oryctolagus cuniculus      | 79.36| 71.36| 75.85| 79.36| 71.36| 75.85| 85.76| 47.54| 26.78| 26.78| 15.32| 7 Mazza and Winterson |
| Procavia capensis          | 87.40| 112.00| 87.40|      |      |      |      |      |      |      |     |      |      |      |      |     | (1984)* [1a] |
| Pteropus lylei             | 84.90| 98.30| 90.40|      |      |      |      |      |      |      |     |      |      |      |      |     | (2008) [2a] |
| Rattus norvegicus          | 73.35| 97.57| 98.12| 6.37 | 4.80 | 10.89|      |      |      |      |     |      |      |      |      |     | Jeffery |
| Rattus norvegicus          | 6.88 | 4.92 | 11.10|      |      |      |      |      |      |      |     |      |      |      |      |     | (2008) [2a] |
| Rhinolophus ferrumequinum  | 79.90| 104.00| 87.90|      |      |      |      |      |      |      |     |      |      |      |      |     | (1989) [1b] |
| Saimiri sciureus           | 90.43| 87.02| 89.95| 90.43| 87.02| 89.95| 12.53| 14.80| 15.45| 8.00 | 5.67 | 4.85 | 5.65 | 5.65 | 44.29| 36.28| 38.71 |
| Sciurus carolinensis       | 7.67 | 4.85 | 5.65 | 7.67 | 4.85 | 5.65 | 44.29| 36.28| 38.71| 4.92 | 4.92 | 9.23 |      |      |      |     | (2008) [2a] |
| Sus scrofa                 | 82.80| 96.00| 87.90|      |      |      |      |      |      |      |     |      |      |      |      |      |     | (2009) [3]c |
| Sylvilagus floridanus      | 92.70| 97.50| 77.90|      |      |      |      |      |      |      |     |      |      |      |      |      |     | (2009) [3]c |
| Tamandua brasiliensis      | 74.70| 98.40| 98.40|      |      |      |      |      |      |      |     |      |      |      |      |      |     | (2009) [3]c |
| Tarsius bancanus           | 91.80| 91.80| 73.80| 102.80| 14.50| 14.50| 14.50| 14.50| 14.50| 14.50| 14.50| 14.50| 14.50| 14.50| 14.50| 14.50| 14.50| Matano et al. (1985) [1] |
| Trichechos manatus         | 52.20| 84.90| 86.30|      |      |      |      |      |      |      |     |      |      |      |      |      |     | (2009) [3]c |
| Tupai a glis               | 82.30| 106.00| 102.00|      |      |      |      |      |      |      |     |      |      |      |      |      |     | (2009) [3]c |
| Tursiops truncatus         | 52.20| 84.90| 77.50|      |      |      |      |      |      |      |     |      |      |      |      |      |     | (2009) [3]c |
| Ukaabariobans gobiensis    | 88.80| 105.00| 88.40|      |      |      |      |      |      |      |     |      |      |      |      |      |     | (2009) [3]c |
| Zalambdalestes lechei      | 81.00| 93.60| 85.60|      |      |      |      |      |      |      |     |      |      |      |      |      |     | (2009) [3]c |
| Zhelestid                 | 88.80| 96.80| 93.10|      |      |      |      |      |      |      |     |      |      |      |      |      |     | (2009) [3]c |
to angular head accelerations may influence semicircular canal orthogonality.

We also find that deviations from canal angle symmetry and coplanarity are negatively correlated with estimated vestibular sensitivity. However, these correlations are weaker and more strongly influenced by phylogeny compared to the results for orthogonality. As a result, phylogenetically controlled analyses of the relationship between estimated vestibular sensitivity and both angle symmetry and coplanarity are not significant (Table 5). These results do not necessarily imply the absence of a functional relationship between canal angle symmetry or coplanarity and vestibular sensitivity, but they do indicate that there is a strong phylogenetically correlated influence on these relationships.

In this context, it is also noteworthy that the obligate fossorial genera in our analysis (Notoryctes, Chrysochloris, Talpa, and Heterocephalus) show greater deviations from canal orthogonality than most non-fossorial genera (Table 2). Indeed, the average 90\textdegree\_\text{rot} value for the 4 fossorial taxa in our sample (mean = 11.0\(\degree\); st. dev. = 3.2\(\degree\)) is twice that of non-fossorial taxa (mean = 5.5\(\degree\); st. dev. = 1.8\(\degree\)). Notoryctes, Chrysochloris, Talpa, and Heterocephalus also share comparatively low estimates of semicircular canal sensitivity (fossorial taxa: Sensitivity\_ave = 0.27–0.48; Sensitivity\_max = 0.38–0.59; non-fossorial taxa: Sensitivity\_ave mean = 0.89, st. dev. = 0.38; Sensitivity\_max mean = 1.10, st. dev. = 0.47; Table 4). While this sample of fossorial genera is small, it is also taxonomically diverse, including a marsupial (Notoryctes), an afrotheria (Chrysochloris), a cipripitphalan (Talpa), and a rodent (Heterocephalus). These data therefore suggest that low degrees of semicircular canal orthogonality and relatively low sensitivity to angular accelerations may have evolved concurrently with a fossorial lifestyle at least 4 times in mammals. Nonetheless, it is not functionally clear why lower degrees of canal orthogonality would be associated with a burrowing lifestyle.

Our findings are consistent with those of Billet et al. [55], who report highly variable and non-orthogonal ipsilateral canal pair angles in three-toed sloths (Bradypus variegatus). Billet et al. suggested that such high variability is the result of diminished selection pressure in slower-moving mammals to maintain orthogonal semicircular canals. Furthermore, the negative relationship between angular head velocities and 90\textdegree\_\text{rot} observed by Malinzak et al. [33] accords well with our finding of a negative relationship between mean vestibular sensitivity and 90\textdegree\_\text{rot} (Figure 4). The combined results of both studies thus show that species with the greatest deviations from canal orthogonality tend to experience slower head rotations during locomotion [33] and to have less sensitive semicircular canals (Figure 4). Although Malinzak et al. [33] based their conclusions on a smaller sample of 11 primate species, their analysis is the only comparative study to date that directly measured angular head velocities produced during locomotion. These authors further concluded that species which regularly encounter higher angular head accelerations during locomotion require more orthogonal canals in order to have more uniform sensitivity to angular accelerations in three dimensions. Here we have shown that the degree to which semicircular canals approach orthogonality is correlated with mean estimated sensitivity to angular accelerations, and that mean sensitivity in turn is solely determined by canal radius of curvature. These findings reinforce the conclusion that both the radii and orientations of the semicircular canals may be influenced by selection related to forces generated during locomotion.

**Acknowledgments**

This research was greatly facilitated by Chris Bell, James Sprinkle and Larry Witmer who reviewed it in dissertation form. Special thanks are due...
to Tim Hullar, who helped immensely in providing and implementing Bubbles.mat, and for conversations describing calculation of sensitivity. We thank editor Andrew Farke and reviewers Justin Georgi and Rich Kay for their assistance in revising the first submission of this manuscript. Thanks also to Charlie Nunn, Dunné Reed, and Sally Amen for statistical advice. Scanning help was graciously provided by Jessie Maisano, Matt Colbert, Rich Ketcham and the staff of the UTCT lab. Mark Coleman, Tim Hullar, Ted Macrini, and Blair Van Valkenburgh gave permission to use high resolution X-ray computed tomographic scans of their specimens for this study.

**Author Contributions**
Conceived and designed the experiments: JCB ECK TBR. Performed the experiments: JCB. Analyzed the data: JCB ECK. Contributed reagents/materials/analysis tools: TBR. Wrote the paper: JCB ECK TBR.

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