

Analysis of intraindividual and intraspecific variation in semicircular canal dimensions using high-resolution x-ray computed tomography

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Abstract

The semicircular canal system tracks head rotation and provides sensory input for the reflexive stabilization of gaze and posture. The purpose of this study was to investigate the intraspecific and intraindividual variation in the size of the three semicircular canals. The right and left temporal bones were extracted from 31 individuals of the short-tailed shrew (*Blarina brevicauda*) and scanned on a high-resolution x-ray computed tomography system. The radius of curvature was calculated for each of the three semicircular canals for each side. Paired *t*-tests and independent sample *t*-tests indicated no significant differences in canal size between the right and left canals of the same individuals or between those of males and females of the same species. Pearson product moment correlation analyses demonstrated that there was no significant correlation between canal size and body mass in this sample.

Key words *Blarina*; inner ear; three-dimensional computed tomography.

Introduction

The bony labyrinth of the mammalian temporal bone houses the sense organs for hearing and balance. The organ of balance is comprised of the otolith system inside the vestibule and the semicircular canal system, a series of membranous ducts enclosed in bony semicircular canals. There are three such canals (anterior, posterior and lateral) that lie roughly orthogonal to one another. Whereas the otolith system deals with linear motion and gravity, the semicircular canal system detects angular changes in head position and provides input for the extraocular and neck muscles for gaze stabilization while an animal moves through the environment (Curthoys et al. 1977a,b; Spoor & Zonneveld, 1998).

Yang & Hullar (2007) recently demonstrated through experimental work a significant and strong correlation between the sensitivity of the canal system and the canal radius of curvature. Specifically, they found that sensitivity increases with increasing canal size as predicted from previous comparative studies and biophysical models (Curthoys et al. 1977a,b; Blanks et al. 1985; Curthoys & Oman, 1986; Spoor & Zonneveld, 1998; Rabbitt et al. 2004). Comparative

analyses of semicircular canal size across primates and other mammals have also established the relationship between locomotor agility and canal size. Relatively agile animals with jerky head motion tend to have large canal radii of curvature relative to body size, whereas those that are slow moving have relatively small radii of curvature (Spoor, 2003; Spoor et al. 2007; Walker et al. 2008; Silcox et al. 2009). Given this functional relationship, there has been significant interest in the semicircular canal system in relation to the locomotor behavior of animals and the reconstruction of behaviors in the fossil record.

One of the common assumptions in studies of semicircular canal variation, and indeed inherent in the experimental work and biophysical hypotheses of labyrinth function (Rabbitt et al. 2004; Yang & Hullar, 2007), is that there is no variation in canal size between the right and left sides of an individual or between males and females of the same species. If there is significant within-individual variation, then studies of the bony labyrinth and its relationship to locomotor behavior would become more complicated. Additionally, many studies of the semicircular canal system use a small number of individuals from each taxon and may not take into account potential sexual dimorphism in canal size, thus assuming relatively low levels of intraspecific variation.

The purpose of this study was to examine intraspecific and intraindividual variation in semicircular canal size using a sample of short-tailed shrews, *Blarina brevicauda*, with known individual body mass and sex. We expected

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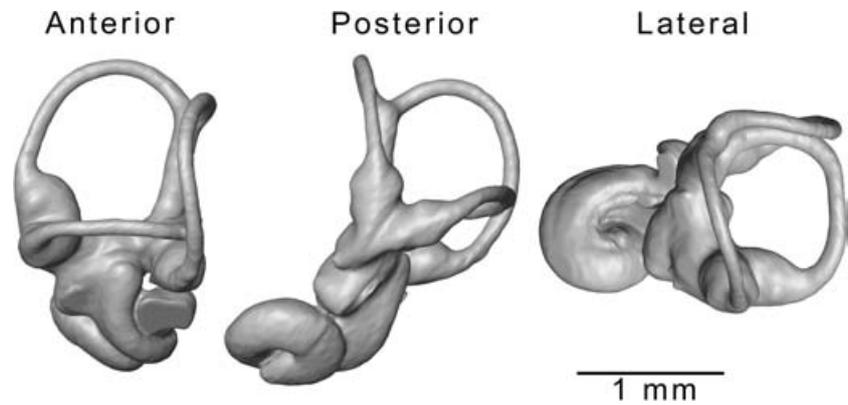


Fig. 1 Three-dimensional reconstruction of the bony labyrinth of *Blarina brevicauda* showing the shape of each canal.

there to be some small amount of fluctuating asymmetry in canal size between the right and left sides but no directional asymmetry between the sides. Previous analyses have found a negatively allometric relationship between canal size and body mass interspecifically among mammals (Jones & Spells, 1963; Spoor et al. 2007) so canal size may also scale with body mass intraspecifically. However, given the limited body size range in this small, monomorphic taxon (Choate, 1972; Braun & Kennedy, 1983), we did not expect to find a significant relationship between canal size variation and body size or between males and females.

Materials and methods

The sample for the current study consisted of a total of 31 *B. brevicauda* specimens collected in and around State College, Pennsylvania, USA, between May and November of 2003 and 2004 for another, unrelated study. Body mass and sex were determined at the time of dissection. To isolate the temporal bones in which the semicircular canals are housed, the skull was first cleaned of all soft tissue by boiling the skull in water and then placing it in a solution of trypsin and sodium borate (30–50 mL of 0.5 g 100 mL⁻¹). After the skulls were cleaned enzymatically of all soft tissue, the temporal bones were removed from the rest of the skull. The entire cleaning process ranged from 70 to 100 days. Following dissection and extraction there were a total of 59 temporal bones from the 31 individuals.

The skeletonized temporal specimens were scanned on the OMNI-X HD600 high-resolution x-ray computed tomography (HRCT) system in the Center for Quantitative Imaging at Pennsylvania State University using the X-TEK microfocus x-ray subsystem. HRCT operates on the same principles as medical computed tomography but it is capable of much higher resolutions down to approximately 0.005 mm on many systems (Denison et al. 1997; Ketcham & Carlson, 2001). The HRCT data produced by the Penn State system are analogous to computed tomography data used by other researchers to measure the size of the semicircular canals in primates and other mammals (Spoor et al. 1994, 2002, 2007; Spoor, 2003; Calabrese & Hullah, 2006; Walker et al. 2008).

Each temporal bone was embedded in a florist foam mount and HRCT scan data were collected for up to 16 temporal bones simultaneously. The specimens were scanned in air with source energy settings of 120 kV and 0.100 mA. Scans were collected with 2400 views, one sample per view, and 41 slices per rotation.

The thickness of each slice was 0.0372 mm. The field of reconstruction was set to 30.72 mm and the image data were reconstructed with a 1024 × 1024 matrix, resulting in a pixel size of 0.030 mm. Following HRCT scanning, each individual temporal bone specimen was cropped from the larger scan dataset using ImageJ 1.36 (<http://rsb.info.nih.gov/ij/>) and saved as a raw image stack.

Image analysis was performed using the visualization software Voxblast (VayTek, Inc., Fairfield, IA, USA). Each temporal bone image stack was resliced along the plane of each canal by fitting a plane to three specified points along the canal arc. Two resliced images were used for the posterior canal because this canal had a slight curvature that prevented use of a single plane in reslicing. Height (H) and width (W) were measured for each canal and the radius of curvature (R) was calculated as $0.5 * (H + W)/2$, following the methods of Spoor & Zonneveld (1998). The canal shapes were roughly circular (Fig. 1) so simple radius of curvature measurements should be sufficient to characterize the canal size (Curthoys et al. 1977b). All canal measurements were collected by a single investigator (K.L.W.).

Paired *t*-tests were used to compare R for each of the three canals from the right and left sides in all individuals to test for directional asymmetry. Independent sample *t*-tests were used to compare R for males and females for all three canals on the right and left sides separately. Pearson product-moment correlation coefficients were calculated to examine the relationship between body mass and canal size for each canal on the right and left sides. Statistical analyses were performed using SPSS 16.0. In all statistical tests, null hypotheses were rejected for *P* values of less than 0.05.

Results

The mean, standard deviation (SD) and coefficient of variation (CV) for each semicircular canal from the right and left sides are listed in Table 1 and displayed in Fig. 2. The lateral canal was the smallest of the three with mean values of 0.625 and 0.626 mm for the left and right sides, respectively. The anterior and posterior semicircular canals were more similar in size and both were larger than the lateral. There were no statistically significant differences in semicircular canal radius of curvature between the right and left side for any of the three canals or the mean (Table 1), demonstrating no directional asymmetry in canal size in this sample. The mean values for right and left canals differed by less than 0.002 mm. The mean

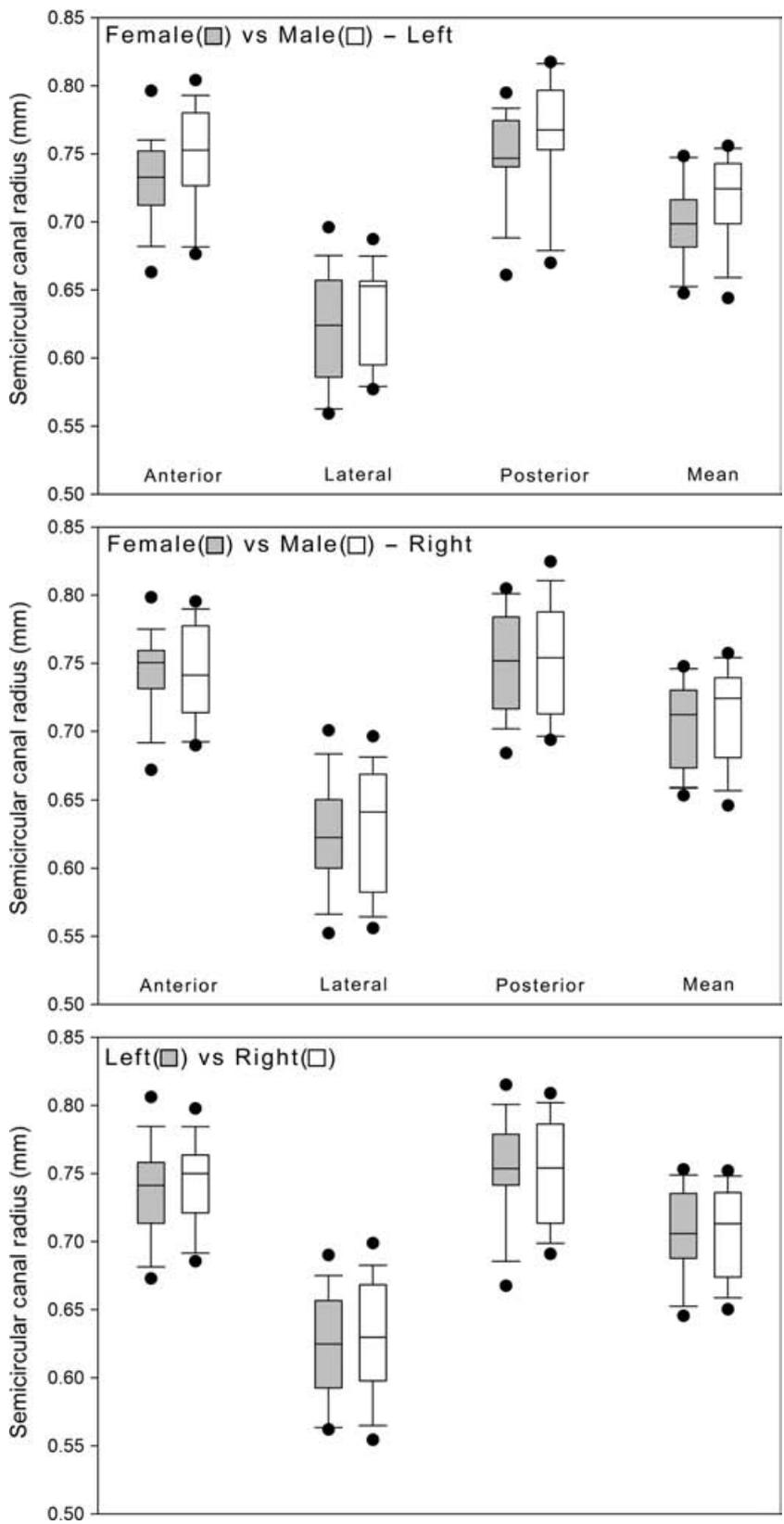


Fig. 2 Boxplots of semicircular canal radius for each canal showing female vs male for left (top) and right (middle) as well as left vs right sides (bottom).

Table 1 Summary statistics and results of paired sample *t*-tests of canal radius for the right vs left side for each canal and the mean of the three canals

Canal	<i>n</i>	Side	Mean (mm)	SD	CV	<i>t</i>	<i>P</i>
Anterior	27	Left	0.738	0.038	5.18	0.013	0.989
	27	Right	0.741	0.037	4.99		
Posterior	28	Left	0.751	0.042	5.60	-0.227	0.823
	27	Right	0.750	0.040	5.33		
Lateral	28	Left	0.626	0.041	6.57	0.121	0.905
	28	Right	0.627	0.045	7.14		
Mean canal	25	Left	0.706	0.033	4.65	-0.631	0.535
	26	Right	0.708	0.034	4.82		

CV, coefficient of variation.

unsigned percent difference between right and left sides was 3% or less (Table 2) although the SDs were quite high. In only one canal was the percent difference higher than 10%.

Summary statistics for the comparison between semicircular canal radius in males and females are listed in Tables 3 and 4 and displayed in Fig. 2. For each of the three canals, the mean values for males were larger than those for females but none of these comparisons were statistically significant for either right or left sides (Tables 3, 4). Canal size was not significantly correlated with body mass for any canals or the mean canal radius for either the right or left sides ($P > 0.05$; Table 5; Fig. 3).

Discussion

Analyses of semicircular canal size variation in relation to body mass and locomotor agility are important not only for understanding the biological function of the vestibulo-ocular and vestibulocollic systems in vertebrates but also for their potential utility in reconstructing locomotor behaviors in extinct taxa. The purpose of the current study was to test some of the common assumptions made in comparative studies of the semicircular canal system, such as bilateral

Table 2 Absolute and percent difference between radius of curvature for each canal from the left (L) and right (R) sides for each individual

Specimen	Anterior		Posterior		Lateral	
	L-R	% difference	L-R	% difference	L-R	% difference
PSU059	-	-	-0.006	0.572	0.003	0.266
PSU060	0.013	1.295	-0.003	0.336	0.025	2.499
PSU061	-0.034	3.440	0.037	3.706	-0.130	13.045
PSU062	-	-	0.077	7.696	0.018	1.781
PSU063	-0.047	4.702	0.015	1.492	-0.068	6.778
PSU064	0.061	6.056	-	-	-	-
PSU065	-0.001	0.108	-0.037	3.728	0.019	1.947
PSU066	0.037	3.711	-0.016	1.581	0.035	3.543
PSU067	-	-	-	-	-0.006	0.566
PSU069	-0.028	2.764	-0.017	1.680	-0.013	1.335
PSU070	0.004	0.395	0.000	0.000	-0.009	0.880
PSU071	-0.019	1.856	-0.030	2.993	-	-
PSU072	-0.013	1.350	-0.063	6.342	-0.025	2.467
PSU073	0.035	3.501	-0.013	1.341	-0.018	1.773
PSU074	-	-	-0.028	2.831	0.039	3.898
PSU075	-0.011	1.119	0.021	2.101	-0.033	3.289
PSU077	0.005	0.463	-0.017	1.662	0.026	2.613
PSU078	-0.051	5.128	-0.007	0.704	-0.025	2.549
PSU079	0.043	4.264	-	-	0.034	3.438
PSU081	-0.006	0.618	-0.034	3.447	0.038	3.842
PSU083	-0.045	4.463	-0.039	3.894	-0.008	0.758
PSU086	0.043	4.313	0.053	5.315	-0.006	0.636
PSU087	-0.015	1.519	0.020	2.035	-0.023	2.347
PSU088	-0.012	1.175	0.061	6.081	0.037	3.663
PSU089	-0.015	1.531	-0.047	4.727	0.035	3.505
PSU090	0.025	2.509	0.042	4.167	0.021	2.086
PSU091	0.031	3.104	-0.015	1.479	0.065	6.535
Mean	0.000	2.582	-0.002	2.913	0.001	3.042
SD	0.031	1.717	0.036	2.045	0.041	2.645
<i>n</i>	23		24		25	

Percent difference was calculated as the absolute value of the difference (left - right) divided by the mean of left and right radii.

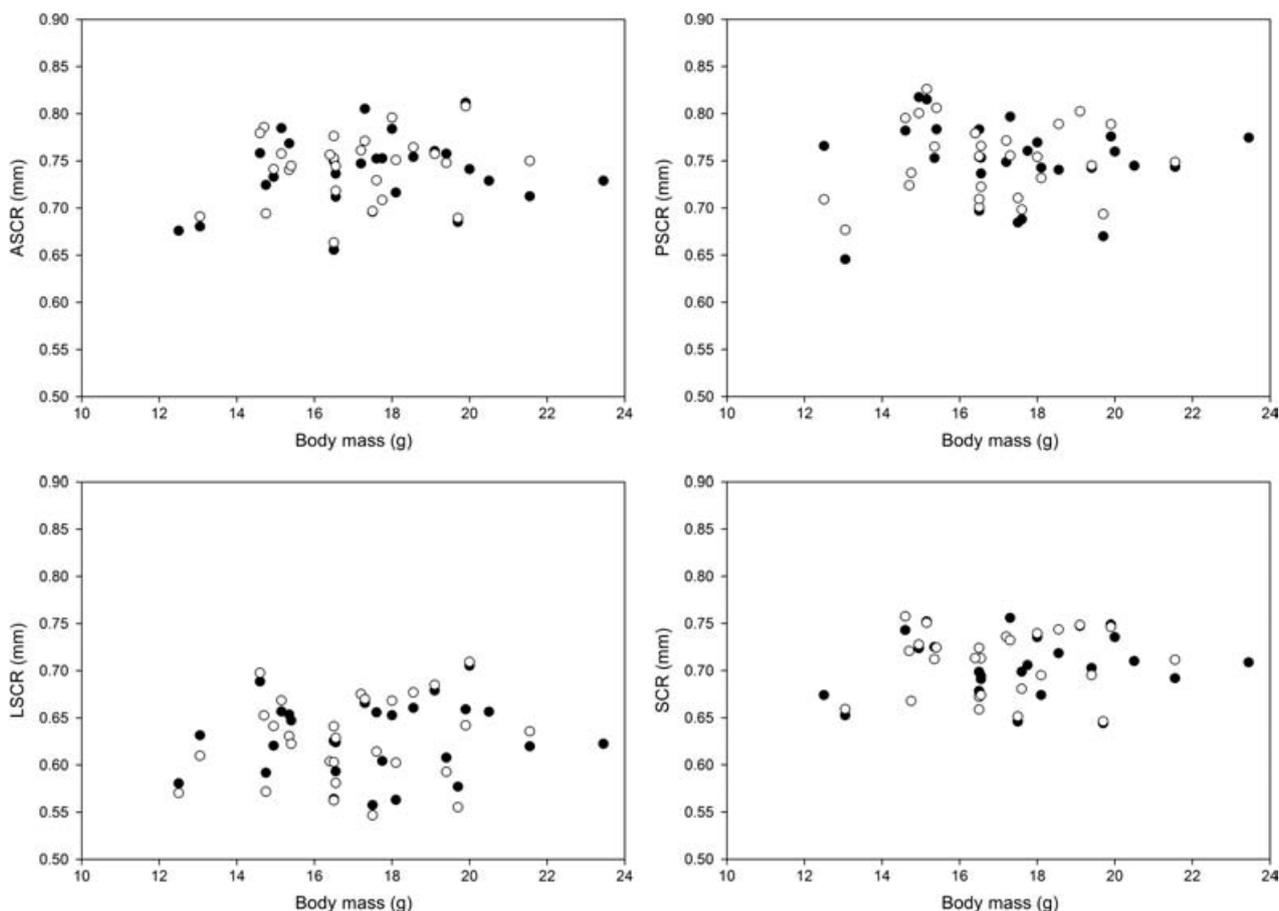


Fig. 3 Bivariate plot of canal radius against body mass for each semicircular canal (anterior, posterior and lateral) and the mean canal. Closed circles, left side; open circles, right side.

Table 3 Summary statistics and results of independent sample *t*-tests of canal radius in males and females for the left side canals

Canal	Sex	<i>n</i>	Mean (mm)	SD	CV	<i>t</i>	<i>P</i>
Anterior	M	11	0.748	0.040	5.35	1.145	0.263
	F	16	0.731	0.036	4.92		
Posterior	M	10	0.762	0.049	6.43	1.003	0.325
	F	18	0.745	0.038	5.10		
Lateral	M	11	0.632	0.038	6.01	0.575	0.570
	F	17	0.622	0.044	7.07		
Mean canal	M	10	0.716	0.036	5.03	1.197	0.243
	F	15	0.700	0.030	4.29		

CV, coefficient of variation.

Table 4 Summary statistics and results of independent sample *t*-tests of canal radius in males and females for the right side canals

Canal	Sex	<i>n</i>	Mean (mm)	SD	CV	<i>t</i>	<i>P</i>
Anterior	M	11	0.745	0.037	4.94	0.149	0.883
	F	16	0.743	0.035	4.73		
Posterior	M	11	0.751	0.044	5.81	0.360	0.722
	F	16	0.750	0.039	5.17		
Lateral	M	11	0.631	0.047	7.53	0.034	0.973
	F	17	0.625	0.044	7.08		
Mean canal	M	10	0.713	0.037	5.19	0.674	0.507
	F	16	0.704	0.033	4.68		

CV, coefficient of variation.

symmetry within individuals, the lack of sexual dimorphism in the absence of distinct body size differences and the independence of canal size from small variations in body mass within a taxon.

The results of the current study justify these common practices. As predicted, there was no directional asymmetry in the canal dimensions between the right and left ears of

the same individuals. A small amount of asymmetry (less than 5% difference) was found, which is to be expected in any biological system. Although not commonly investigated, bilateral symmetry in canal dimensions is certainly implied in the biophysical models of canal function. Significant asymmetry, greater than that found in this study, would have raised issues in relation to the way that

Table 5 Pearson product-moment correlation coefficients for canal size and body mass for each semicircular canal and the mean canal radius for each side

Canal	<i>n</i>	Side	<i>r</i>	<i>P</i>
Anterior	27	Left	0.180	0.370
	27	Right	0.166	0.407
Posterior	28	Left	-0.005	0.978
	27	Right	0.081	0.687
Lateral	28	Left	0.135	0.493
	28	Right	0.163	0.406
Mean canal	25	Left	0.111	0.598
	26	Right	0.048	0.815

afferent signals from bilateral canals are processed, e.g. as sensory output of the vestibulo-ocular reflex, as each side would presumably have different sensitivities to angular displacements.

Blarina brevicauda is not a significantly dimorphic species (Choate, 1972; Braun & Kennedy, 1983) although the females in this sample were slightly larger than the males ($t = 2.394$; $P < 0.05$). Even with the slight body mass difference, no significant differences in canal size were found between males and females, indicating no sexual size dimorphism in canal dimensions. Additionally, no significant relationship was found between canal size and body mass in this analysis. This result is not particularly surprising considering the narrow body size range in this sample and the strong negatively allometric relationship between canal size and body mass in mammals interspecifically (Spoor et al. 2007). The size of the semicircular canals is fixed relatively early during the development and ossification of the otic capsule (Anson & Bast, 1949), as demonstrated statistically by Jeffery & Spoor (2004). Variation in adult body mass probably results from both genetic and epigenetic effects, the former of which would also presumably act on overall labyrinth size.

Given the relatively small sample sizes used here, our analyses have low statistical power, suggesting the possibility that we might not be able to detect significant relationships in our dataset, were they to exist. However, given the miniscule effect sizes that we observed, inordinately large sample sizes would be necessary to attain the level of statistical power considered adequate to reject a false null hypothesis [0.8 according to Cohen (1977)]. Our bilateral and intersexual comparisons had effect sizes ranging from 0.024 to 0.483, thus with an alpha level of 0.05 and statistical powers ranging from 0.051 to 0.205. Although most required sample sizes are in the hundreds or thousands of individuals, in the case of the former, 54 270 shrews would be necessary to achieve a power of 0.8. Clearly, this is not feasible. No published intraspecific correlation between semicircular canal radius of curvature and body mass exists. Thus, there is not a known population cor-

relation to use as an effect size in such a power analysis. This fact further underscores the importance of the present study. Although the interspecific correlations calculated by Spoor et al. (2007) (range 0.367–0.506) are much higher than those observed here (range -0.005–0.180), they might not be adequate expectations for the intraspecific correlations measured here. Given these concerns, we present our data graphically (Figs 2, 3) to illustrate the lack of any relationship or pattern among variables in our dataset.

The results of the current study have important implications for interspecific comparative analyses of semicircular canal dimensions in extant and extinct vertebrates. Recent work on the morphology of the inner ear of mammals strongly suggests a functional link between semicircular canal dimensions and locomotor agility, specifically the jerkiness of head motion during locomotion (Spoor et al. 2007; Walker et al. 2008; Spoor & Thewissen, 2008). This recent work by Spoor and colleagues using a large, diverse taxonomic sample provided strong quantitative support for a concept that has been suggested from qualitative and quantitative work since early in the last century (Gray, 1907, 1908; Jones & Spells, 1963; Takahashi & Minatoya, 1972; Takahashi, 1976; Matano et al. 1985, 1986; Spoor et al. 1994, 2002; Spoor & Zonneveld, 1995, 1998; Spoor, 2003). Additionally, reconstructions of locomotor behaviors in extinct taxa frequently must rely on a single specimen or at most only a few specimens. As a result, analyses of extinct taxa frequently cannot account for intraspecific variation. One potential limitation of much of this previous work is the lack of large samples to evaluate intraspecific variation.

The results of this study provide additional insight into intraspecific variation in canal size in mammals. The variation in *Blarina* canal dimensions found here is quite similar to that found for a diversity of other mammals reported in the literature. The means, SDs and CVs for the radius of curvature for each of the three semicircular canals from a variety of mammals are listed in Table 6. The CVs from these diverse mammalian taxa generally fall below 10, suggesting a relatively limited amount of intraspecific variation in canal size for all three canals. The CVs for the *Blarina* sample from the current study are 4.66, 4.97 and 6.42 for the anterior, posterior and lateral canals, respectively, which is well within the range of CVs for other mammal species of various sizes.

In general, it appears that intraspecific variation in canal size is relatively low and broadly similar across a range of mammalian taxa. Among the studies sampled in Table 6, the lowest CV is 3.20 from the posterior canal of *Macaca mulatta* reported by Blanks et al. (1985), whereas the highest CV of 10.38 is found for the posterior canal of *Pongo pygmaeus* reported by Spoor & Zonneveld (1998). The species mean body masses among these taxa range from approximately 17 g in *B. brevicauda* to 120 kg in *Gorilla gorilla* but there do not seem to be any size-related effects on the amount of canal size variation within each taxon.

Table 6 Mean, SD and coefficient of variation (CV) for each semicircular canal from a variety of mammalian species

Taxon	Anterior			Posterior			Lateral			n	Source
	Mean	SD	CV	Mean	SD	CV	Mean	SD	CV		
<i>Blarina brevicauda</i>	0.74	0.03	4.66	0.75	0.04	4.97	0.63	0.04	6.42	31	This study
<i>Cavia porcellus</i>	2.04	0.19	9.31	1.69	0.14	8.28	2.43	0.20	8.23	10	Curthoys et al. (1977a)
<i>Cryptomys</i> sp.	1.21	0.05	4.13	0.95	0.04	4.21	1.05	0.04	3.81	8	Lindenlaub et al. (1995)
<i>Gorilla gorilla</i>	2.90	0.16	5.52	3.10	0.27	8.71	3.10	0.23	7.42	6	Spoor & Zonneveld (1998)
<i>Homo sapiens</i>	3.20	0.24	7.50	3.10	0.30	9.68	2.30	0.21	9.13	53	Spoor & Zonneveld (1998)
<i>Homo sapiens</i>	3.86	0.27	6.99	3.58	0.16	4.47	2.80	0.28	10.00	10	Curthoys et al. (1977a)
<i>Macaca fascicularis</i>	2.40	0.16	6.67	2.20	0.17	7.73	2.20	0.18	8.18	3	Spoor & Zonneveld (1998)
<i>Macaca mulatta</i>	2.72	0.12	4.41	2.50	0.08	3.20	2.41	0.15	6.22	10	Blanks et al. (1985)
<i>Pan paniscus</i>	2.60	0.19	7.31	2.50	0.16	6.40	2.40	0.18	7.50	6	Spoor & Zonneveld (1998)
<i>Pan troglodytes</i>	2.70	0.20	7.41	2.80	0.24	8.57	2.40	0.24	10.00	7	Spoor & Zonneveld (1998)
<i>Pongo pygmaeus</i>	2.70	0.23	8.52	2.60	0.27	10.38	2.40	0.10	4.17	7	Spoor & Zonneveld (1998)
<i>Rattus norvegicus</i>	1.52	0.05	3.29	1.20	0.04	3.33	1.14	0.04	3.51	8	Lindenlaub et al. (1995)
<i>Saimiri sciureus</i>	2.18	0.09	4.13	1.78	0.07	3.93	1.86	0.12	6.45	10	Blanks et al. (1985)
<i>Spalax ehrenbergi</i>	1.48	0.06	4.05	1.18	0.04	3.39	1.31	0.05	3.82	8	Lindenlaub et al. (1995)
Mean CV			5.99			6.23			6.78		

These data also provide insight into variation in canal size in sexually dimorphic species. The most dimorphic of the primate species in the sample in Table 6 are *Gorilla* and *Pongo*, with males being on average more than twice the size of females. With both of these primate samples equally represented by males and females (Spoor & Zonneveld, 1998), the CVs for these taxa do not appear any higher than those of the moderately dimorphic or monomorphic taxa listed.

The absence of intraindividual variation and the lack of sexual dimorphism and body size effects on canal dimensions demonstrated by the current analysis lend at least conditional support to the common use of pooled species mean values of canal size in comparative studies. The possibility does exist that the small body mass of the *Blarina* used in this sample has an effect on the relationship between canal size and body mass. There is no evidence from interspecific analyses such as Spoor et al. (2007) to suggest that the scaling relationship between canal size and body mass differs depending on body size but more data from a diverse taxonomic sample of small-bodied animals would be required to address the scaling relationships in such animals. Similar studies using samples with known sex and body mass covering a wider taxonomic and body size range are clearly warranted to elucidate further the significance of intraspecific variation in inner ear morphology at various body sizes.

Conclusions

The radius of curvature of the three semicircular canals was found not to vary significantly within a single-species sample of short-tailed shrews, *B. brevicauda*. The semicircular canals in this taxon were found to be bilaterally symmetrical

within individuals, not sexually dimorphic and not affected by small variations in body mass across individuals. These results strongly support the use of species means and small samples for analyses of semicircular canal size variation in extant vertebrates and for reconstructions of locomotor behavior in extinct taxa.

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Author contributions

All three authors contributed to the design and conception of the study, data analysis and interpretation, and manuscript preparation.

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