Brain Geometry and its Relation to Migratory Behavior in Birds

R. Fuchs[1], H. Winkler[2], V. P. Bingman[3], J. D. Ross[4] and G. Bernroider[1,*]

[1]*Department of Organismic Biology, Neurosignaling and Neurodynamics Unit, University of Salzburg, Austria*

[2]*Konrad Lorenz Institute for Comparative Ethology, Wien, Austria*

[3]*Department of Psychology and J.P. Scott Center for Neuroscience, Mind and Behavior, Bowling Green State University, Bowling Green, Ohio, USA*

[4]*Oklahoma Biological Survey, University of Oklahoma, Norman, Oklahoma, USA*

Abstract: A central concern in neuroscience can simply be brought down to the question of how a brains organization relates to its great diversity of functions. It is generally agreed that this relation must be based on multiscale organizational principles, ranging from the macroscopic level of the entire organ down to the cellular and molecular level. The functional correlates may also be seen as hierarchical constructs ranging from phylogenetic constraints and selectable life history traits down to perception, action and cognition. Here we focus on the relationship between macroscopic brain measures and a conspicuous life history variable in many animal species, migration. Migratory songbirds tend to have smaller brains than resident species. However, in the absence of data providing a detailed mapping of variation in brain subdivisions onto variation in migratory behaviour, offering a causal interpretation of the observed difference in brain size is difficult. Here we describe a set of large scale, geometric measures, which, despite different phylogenetic affiliations, discriminate migratory status across multiple avian lineages and eco-geographical regions. We build our investigation on complete, serial-section based, 3-D volumetric reconstructions of telencephalic subdivisions involving four song bird genera, which differ in their migratory status: long distance (more than 3000 km) and modest or no (0-3000 km) migratory behaviour. Our findings suggest that migratory behaviour as a population level trait can be discriminated at the level of geometrical forebrain measures. We finally discuss the results with respect to the developmental patterns that are largely responsible for the observed differences in brain geometries.

Keywords: Neuroecology, Neurodevelopment, Brain geometry, Allometry, Encephalization, Telencephalization, Migratory behaviour, Population level phenomena, Life-history variables, Structure-function correlations.

INTRODUCTION

A cornerstone of the growing field of 'Neuroecology' [1] is the observation that variation in brain size and relative organization of brain structures ('cerebrotypes') correlate with adaptive variations in behaviour. The correlation is often discussed with respect to a set of behavioural traits supported by what is referred to as 'executive' or 'cognitive' functions [2-4]. The defining characteristics of behaviour supported by 'executive functions', and the brain structures that regulate them, is the capacity for behavioural innovations that is assumed to i) facilitate flexible and novel responses to cope with environmental challenges [5, 6] and ii) support complex social interactions (as described initially by the 'social intelligence hypothesis' in primates [7] and the more general 'social brain size hypothesis' as suggested by Dunbar and Shultz [8, 9]).

The correlation between brain organization and ecological life-history variables finds a highly conspicuous and almost paradigmatic challenge in the study of migration. For an evolving sedentary phenotype, we expect selective pressure to favour adaptations that cope with the changing demands associated with highly seasonal environments. On the other hand, for an evolving migratory phenotype, there could be selective pressure to favour adaptations that enable animals to efficiently 'escape' from the challenges of a seasonal environment by migrating twice each year. Beginning with our initial finding that migratory passeriform species tend to have smaller brains than resident species [10] a number of attempts have been made to identify differences in brain organization that may co-vary with migratory behaviour [11-13]. However, the observed divergence in brain size between sedentary and migratory passerines is still poorly understood at the brain organizational level. A more causal understanding among the involved variables will require a more detailed mapping of variation in brain structures and their known functions onto variation in migratory behaviour (*e.g*. for a critical review of this general approach, see [14]).

Here we examine the relationship between brain organization and migratory behaviour in a sample of passerine species. We build our investigation on serial

*Address correspondence to this author at the Department of Organism Biology, Neurosignaling Unit, University of Salzburg, Hellbrunnerstr 34, A-5020 Salzburg, Austria, E-mail: Gustav.Bernroider@sbg.ac.at

E-ISSN: 2409-3564/14

sections based 3-D volumetric reconstructions of telencephalic subdivisions. In particular, we show that both, scalable and absolute brain size frequently correlate with migratory behaviour in different taxa. A residual based measure of the 'general' encephalization quotient 'EQ' [15] calculated across the sample species supports the expected deviation from the overall allometric regression, with generally larger observed brain volumes in sedentary compared to long distance migratory birds. Further, the present 3-D analysis of pallial and subpallial forebrain structures allows us to establish a '*specific telencephalization quotient*' (sTQ) based on phylogenetically corrected, generalized least squares, and PGLS residuals derived from log-log regressions between telencephalic volumes and their sub-regions [16]. This measure quantifies the difference between an observed regional volume of the telencephalon (*e.g*. hyper-, meso- and nidopallium) and the expected regional volume as predicted from the size of the telencephalon after correcting for phylogenetic correlations.

Overall, the results suggest a differential effect of migratory status on forebrain regionalization. We find that pallial regions, derived from the so-called dorsal ventricular ridge DVR [17], are smaller than expected in long distance migrants. In contrast to DVR structures, dorsal pallial regions (hyperpallium) seem to be larger than expected in long-distance migrants (LD) when compared with sedentary or short distance migrants (SD). As the observed deviations from the allometric expectation are consistent with findings on developmental differences across different ventricular subdivisions of the telencephalon [18], we discuss our findings in view of the timing of neurogenesis and functional regionalization.

MATERIALS AND METHODS

We provide measurements from post-mortem brain samples collected from perfused animals during the last decade from different sources. All donations and collections were carried out with permissions from the appropriate government agencies, including the city of Vienna (MA22–3472/2002), the state of Burgenland, Austria (5-N-A1007/152–2002, 5-N-A1007/195-2003, 5-N-A1007/226-2004, 5-N-A1007/248-2005, 5-N-A1007/295-2007, 5-N-A1007/331-2007), the province of Andalusia, Spain (SCFFS/AFR-CMM R.S.: 232/04), Nebraska Game and Parks Commission, the Texas Wildlife Department and the US Fish and Wildlife Service.

Species used for the present study are given in Table **1.**

Table1: Species and Number of Samples (n), Migration Distance (MD in Thousands of kms), Body Weights (W, Means ± SEM), Mean Wet Brain Volumes (BV, Means ± SEM) and NCBI – GenBank Accession Numbers for Short Distance Migrants (SD, < 3000 km) and Long Distance Migrants (LD, > 3000 km) Across the Four Genera and Fifteen Species of Passeriform Birds Studied

Species(n)		MD	W(g)	BV (mm^3)	GenBank
Acrocephalus melanopogon (3)	SD	0.67	11.67 ± 0.78	534 ± 31.9	AJ004767
Acrocephalus palustris (2)	LD	7.80	11.70 ± 0.70	558 ± 2.0	AJ004774
Acrocephalus scirpaceus (10)	LD	5.20	11.37 ± 0.34	523 ± 4.8	Z73483
Acrocephalus schoenobaenus (8)	LD	5.90	11.47 ± 0.26	523 ± 11.7	Z73475
Chondestes grammacus, mig. (11)	SD	1.50	28.53 ± 0.97	767 ± 18.4	AF255704
Chondestes grammacus, sed. (5)	SD	0.10	25.96 ± 0.56	722 ± 30.2	AF255704
Saxicola torquatus axillaries (5)	SD	0.10	20.68 ± 1.57	604 ± 16.2	EU421093
Saxicola torquatus maura (4)	LD	6.00	13.95 ± 1.23	434 ± 18.1	AY286399
Saxicola torquatus rubicola (4)	LD	3.00	13.50 ± 0.27	531 ± 10.8	AY286398
Sylvia atricapilla (11)	SD	2.40	18.36 ± 0.48	738 ± 29.8	Z73494
Sylvia borin (6)	LD	6.60	20.67 ± 0.67	684 ± 19.5	AJ534549
Sylvia communis (6)	LD	5.25	15.02 ± 0.46	629 ± 45.0	AJ534538
Sylvia curruca (1)	LD	4.80	10.76 ± ----	581 ± ----	AJ534536
Sylvia melanocephala (5)	SD	0.75	10.71 ± 0.19	527 ± 13.4	AJ534544
Sylvia undata (2)	SD	0.75	7.55 ± 0.25	452 ± 15.5	AJ534542

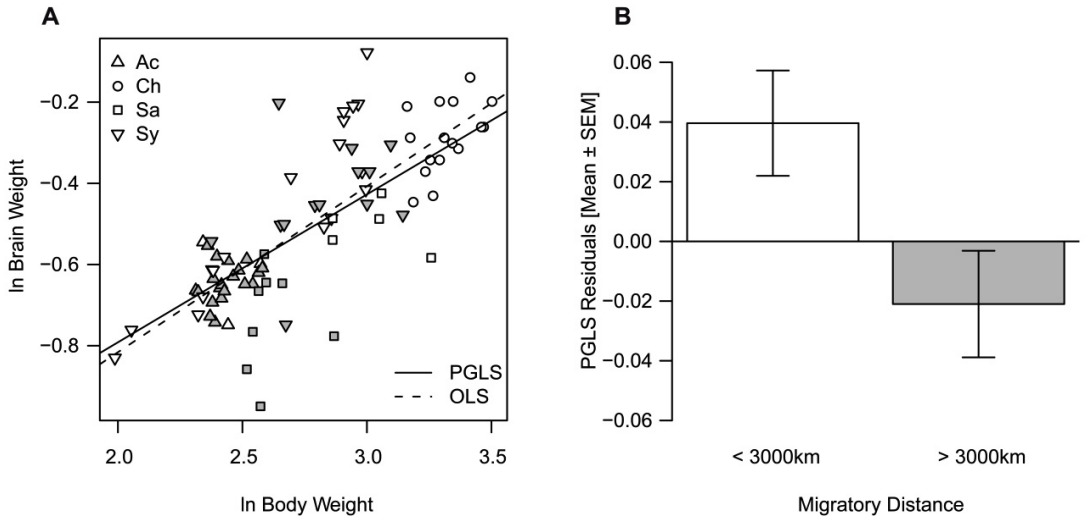

Figure 1: Brain size scales allometrically with body size **(A)** across the four genera of passeriform birds, *Acrocephalus* (Ac), *Sylvia* (Sy), *Saxicola* (Sa) and *Chondestes* (Ch). Dashed line gives the uncorrected least squares regression, the continuous line the phylogenetically corrected generalized least squares (PGLS) regression (coefficient = 0.23, p = 0.0052, df = 81). In **(B)** brain size residuals from the PGLS regression in **(A)** are shown for the short distance (SD) group (n=45, less than 3000km migration) and the long distance (LD) group (n = 38, more than 3000 km migration distance) (t = - 3.148, df = 80, p = 0.0026).

All somatic and brain measurements taken were tested and corrected for phylogenetic correlations, following the methods of Felsenstein and Pagel's generalized least squares (PGLS) procedures [19, 20]. Cyt-b gene sequences for *S. t. axillaris* were kindly provided by Carlos Illera. All other sequences were retrieved from the NCBIGenBank. A matrix of pair-wise sequence distances was computed with the nucleotide substitution model of Tamura and Nei [21] and the phylogenetic tree topology and branch lengths were reconstructed using the BIONJ algorithms [22]. All procedures were carried out with R (vs 2.8.0, R development core team (2008)), including the 'phylogeny extension APE' [23]. The regression model (GLS) between different brain structures and migratory distance was optimized with different phylogenetic correlation matrix methods employing a Bayesian Information Criterion (BIC). At the end this favoured the Brownian motion model [16]. The expected covariance matrix of error terms was established according to $V_{i,j} = \gamma \cdot \Delta t_{i,j}$ where $\Delta t_{i,j}$ denotes the distance in the phylogeny between the root and the most recent common ancestor of taxa *I* and *j,* and the constant γ is the variance of the underlying Brownian motion evolution.

Perfused brains were removed and stored in 4% PFA for a minimum of 24h. Brain volumes were determined by taking the weight of water-volume displaced after passive immersion on a digital balance with a resolution of 1mg. Following volume measurements, several non-invasively accessible linear dimensions were measured using a digital of calliper with 0.01 mm resolution as reported previously [10]. The linear distances were taken along the exposed orthogonal extensions of the basically convex shaped brain structures of the forebrain (3 orthogonal distances), tectum (2 distances) and cerebellum (3 distances). The measured orthogonal dimensions (medio-lateral,dorso-ventral and rostro-caudal) span up 2-dim projection planes with the smallest rectangle containing the structure (See Figure **2**). The obtained forebrain projection planes (frontal, horizontal and sagittal) coincide with the defined 'section planes' in the canary brain, the horizontal plane forming a roughly 45^{o} angle with the horizontal skull axis and 'bill plate' [24].

For volumetric reconstructions, complete series of uni-hemispheric, sagittal sections from 19 birds were obtained using a vibratome and a section thickness of 60 μm. Sections were mounted on coated slides in distilled water and dried at 4^{o}C in a refrigerator for 24h. As the brains were neither dehydrated nor embedded prior to section mounting, tissue shrinkage was small, *i.e*. the 'shrinkage factor' (V_{rec}/V_{nat}) = 0.884 ± 0.014. Sections were subsequently Nissl stained using toluidine-blue, and coverslipped in Neomount. Images from serial-sections were taken at 10x magnification with a digital camera. From the number of sections obtained for each sampled brain hemisphere (between 93 to 119 single sections), every fourth section was selected for alignment using the software 'Reconstruct' [25] resulting in a 'virtual section thickness' of 240 μm

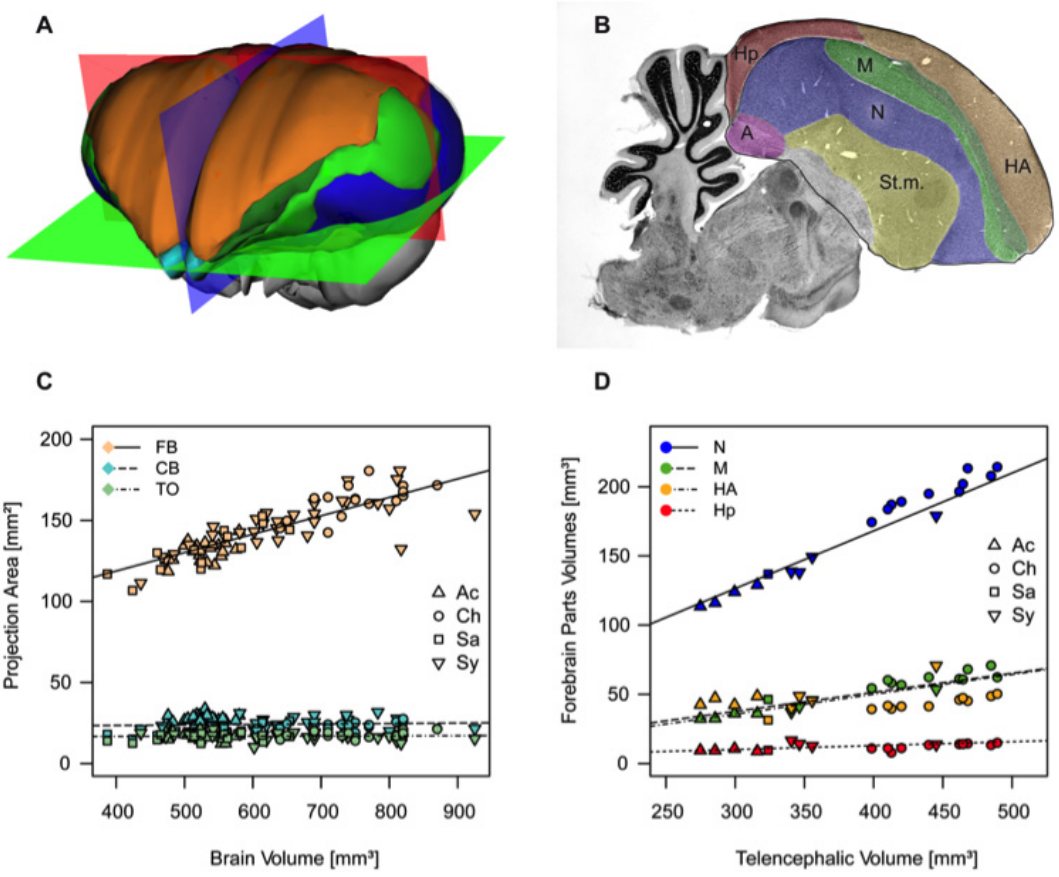

Figure 2 (A-D): An example of a 3D brain reconstruction from *Sylvia atricapilla* (European black cap) **(A)** with colour codes of forebrain regions as shown in medial-saggital section **(B).** In **(C)** we find that the cerebellum (0.100 ± 0.017), the tectum opticum (0.110 ±0.013) and the brainstem (0.130 ± 0.012) occupy a more or less constant fraction of the brain volume, but a non-invasively accessible forebrain measure, as described under methods, shows a clear increase with an increasing brain volume (continuous line gives the PGLS regression with coefficient 73.5 mm^2± 11.37, p< 0.001). In **(D)** this increase in forebrain volume is found to be mainly due to an at least three-fold increase in the volume of the nidopallium compared to meso- and hyperpallium and hippocampus across the four genera studied.

per layer. All forebrain sub-divisions were manually traced with a digitizing tablet (WACOM).

RESULTS

Brain Allometry and Cephalization Quotients

As with other parts of the body, brain size (bw) generally scales allometrically with body size (BW). Among our sampled songbirds we find that relation to be

log bw = -0.708 + (0.407 . log BW), (p< 0.001), R^2 = 0.613 if uncorrected,

and log bw = -1.188 + (0.232 . log BW), (p< 0.005), in the PGLS corrected

version (Figure **1A**); Allometries however are derived from integrated 'rate laws', which establish proportionality between specific growth rates. Specific growth rates are under special developmental control in the brain and can be independent of the development of overall body mass. This sets a limit to the functional and comparative interpretation of relative brain size and has led to the introduction of internal references for brain structures. The *encephalization quotient* (EQ) measures the systematic deviation from the expected value for brain size given a certain body size. In Figure **1B** we show the residuals from brain weight - body weight relations that essentially contain the same information as EQ quotients. In order to account for taxa dependent shifts in the basic allometric regression, we based the analysis on residuals obtained from phylogenetic generalized least squares (PGLS). These are found to be normally distributed (Kolmogorov-Smirnov Test, n=83, p= 0.758) with equal variances (F-Test, d.f.$_1$=41, d.f.$_2$=40, p = 0.990). Figure **1B** compares sedentary birds and short distance

migrants (n = 45) to long distance (>3000 km) migrants (n= 38). As expected, the residual based EQ estimation is found to be significantly higher (positive residuals) for the no/short distance group (t = 3.148, d.f. = 81, p = 0,002).

Specific Volumes and Cerebrotypes

Specific volume fractions ('cerebrotypes') among different brain parts may provide a more relevant measure for brain comparisons because they can be related to functional roles and are independent of body size variations. Our results show that sub-telencephalic structures occupy a more or less constant fraction of the brain volume (Figure **2C**); *e.g*. the cerebellum (0.100 ± 0.017), the tectum opticum (0.110 ± 0.013) and the brainstem (0.130 ± 0.012). These values are close to the results reported from comparisons of volume fractions obtained for many different mammalian taxa, *e.g*. 0.13 ± 0.02 for the cerebellum in mammals (Clark *et al*., 2001). In contrast to these highly conserved sub-telencephalic structures, the size of the forebrain, irrespective of migratory phenotype, shows a clear increase with increasing brain volume (Figure **2C**). As shown in Figure **2D**, this rise is due to an at least three-fold increase in the volume of the nidopallium (allometric coefficient ± std. error =0.4843 ± 0.02, p< 0.001), compared to mesopallium (0.1669 ± 0.01, p< 0.001),hyperpallium (0.03322 ± 0.02, p = 0.20) and hippocampus (0.01828 ± 0.007, p = 0.018).

Generally, telencephalon volume turns out to be a good linear predictor for all pallial regions except the hyperpallium. As mentioned above, an increase in forebrain volume is mainly caused by an increase in the volume of the nidopallium. From 3-D reconstructions of the entire brain (one example is given in Figure **2A**), it becomes apparent that the nidopallium mainly extends as a medio-lateral protrusion within the present passeriformcerebro type (blue colours in Figure **2A,B**). As a consequence this lateral extension increases the horizontal projection plane of the telencephalon (green in Figure **2A**) and provides the main contribution to the brain volume allometry shown in Figure **2C.**

Specific Telencephalization Quotients and Migratory Status

Across the present selection of species, the average annual single migration distance varied between 0 (*e.g*. African *Saxicola torquata*, Texas resident *Chondestes grammacus*) and about 8000 km (*e.g*. *Acrocephalus palustris* and Siberian *Saxicolla torquata*). All species can be assigned a similar cerebrotype (type four out of five, according to the classificaton of Iwaniuk and Hurd [28] with passerines and parrots showing proportionally larger nidopallial, mesopallial and striatopallidal proportions of the telencephalon). The question is whether, within this cerebrotype and the phylogenetic relations introduced by the present selection of species, a behavioural trait such as migratory status can predict aspects of gross brain organization. We find that in a PGLS regression model there is a tendency but not quite significant correlation between absolute brain weight and migration distance (-0.022 ± 0.012, p = 0.074). However, a significant decline for the first principal component (PC1) along migration distance, calculated from 9 morphometric variables that measure brain volume, three orthogonal forebrain extensions, three cerebellar extensions and two tectal extensions as explained under methods, can be found (-0.037 ± 0.014, p = 0.0127). This PC1 explains 42.6 % of the total variation and the correlation with PC1 ('factor loading') is again highest for brain volume (0.830) and horizontal forebrain extension (0.248).

As the above findings revealed evidence for a varying relationship among different forebrain regions with migratory status, it was important to examine deviations from the expected values predicted from the total size of the telencephalon for specific telencephalic volume fractions. We estimated the quotient 'observed regional telencephalic volume' divided by 'expected telencephalic regional volume' from residuals derived from a PGLS regression for six telencenphalic subdivisions (slopes and p-values are provided in Table **2**).

Table 2: Slopes and p-Values from Double ln-Regressions between Different Forebrain Regions Andtelencephalic Volume According the Model: in (Structure) = ln(B) + A × ln (Telen), (left, after Phylogenetic Corrections Based on Pagel [20] and Right, Uncorrected Values)

	PGLS Pagel		Uncorrected	
	Slope	**P-Value**	**Slope**	**P-Value**
Nidopallium	0.9954	<0.0001	1.1422	<0.0001
Mesopallium	1.0390	<0.0001	1.3098	<0.0001
Hyperpallium	1.2379	<0.0001	0.2495	0.2122
MD/HD	0.8177	0.0005	0.3861	0.0108
Hippocampus	0.8616	0.0162	0.5957	0.0167
Arcopallium	0.6288	0.0363	0.9991	<0.0001
Striatum	0.8271	<0.0001	1.1132	<0.0001

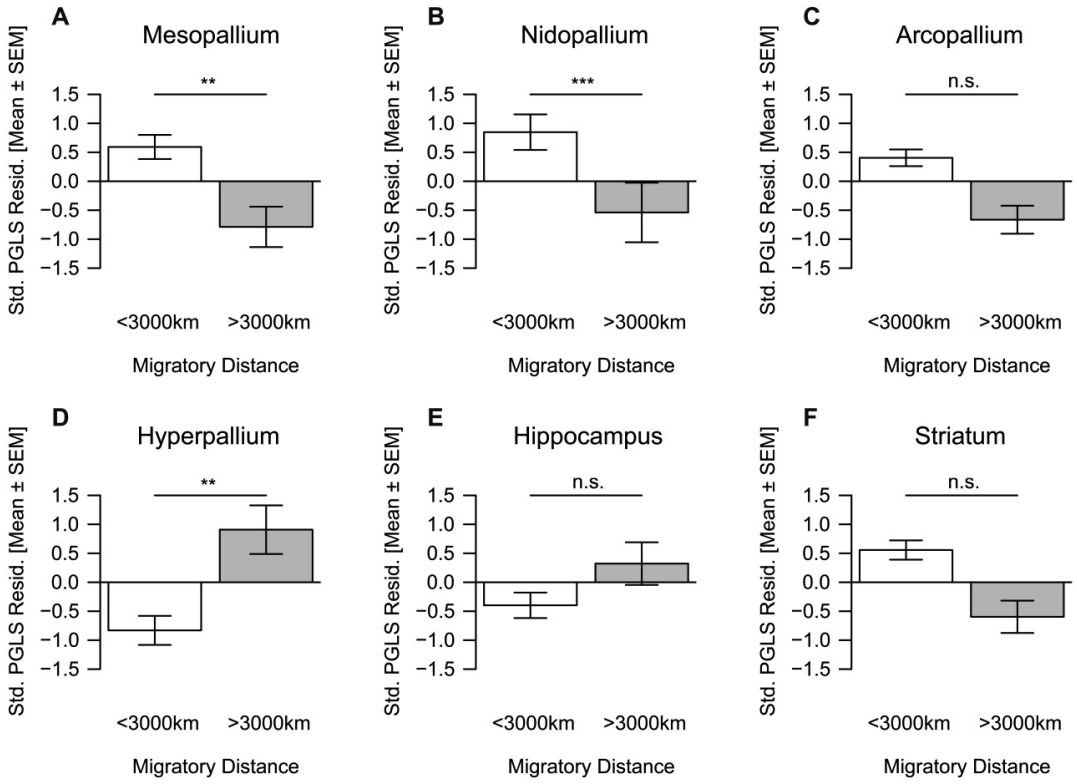

Figure 3 A-F: Residuals from phylogenetically corrected generalized least square regressions (PGLS, Table **2**), using the telencephalon as a predictor for different forebrain regions, are compared between short distance (SD) migrants (left columns, white) and long distance (LD) migrants (right columns, grey). The residuals provide an estimation of regional volume deviations from the prediction based on an allometric relation. Mesopallium (A, p = 0.002), nidopallium (B, p = 0.0003) show a significant increase in SD birds compared to LD birds, with the same tendency in arcopallium (C, albeit n.s. with p = 0.094), whereas hyperpallium (D, p = 0.003) is larger than expected in long-distance migrant birds.

The measure used in Figure **3 (A-F)** could be named 'specific telencephalic quotient' (sTQ) in analogy to the encephalization quotient. A comparison between SD (< 3000 km) birds and LD birds (> 3000 km) reveals that structures that compose the dorsal ventricular ridge (DVR) are generally larger than expected in the SD group (Welch two-sample *t*: mesopallium, $p = 0.002$; nidopallium, $p < 0.001$). By contrast, the hyperpallium appears to be larger than expected in LD animals as compared to short distance migrants ($p = 0.003$). Similar to the hyperpallium, hippocampal telencephalization seems to be slightly increased in long distance migrants, but this increase is not significant when compared to residuals based on the telencephalic volume fraction ($p = 0.16$). However, a principal component analysis using the PGLS residuals of Figure **3** and provided in Table **3**, reveals that the PC1 component (explaining 64 % of total variation) loads negatively on hippocampus (loading factor = - 0.35) and hyperpallium (-0.80). The negative regression of this 'residual PC1' along migration distance is highly significant ($p < 0.01$ for the intercept and$p < 0.0001$ for distance). Thus PC1, derived from residual measures of region-specific telencephalization, decreeses with migration distance and is negatively related to hyperpallial and hippocampal volume fractions, *i.e*. long distance migrants (with low PC1 values) tend to have a higher hippocampal and hyperpallialtelencephalization quotient. Similar to DVR regions the subpallial medial and lateral striatum (Str) also scales larger in SD animals, but this difference is only marginally significant ($p = 0.06$). Also similar to DVR derived pallial structures, the Str loads positively on PC1 from PGLS residuals.

DISCUSSION

Our main finding is that forebrain geometry correlates with migratory status in passeriform birds. A relationship between brain and migration can be found within both sets of allometric relationships, one using body weight as a size reference (as with the encephalization quotient), the other building on the brain or parts of the brain as reference (as with the specific telencephalization quotients). In both cases, resident or short distance migrants have larger brains or

Table 3: Factor Loadings and Proportions of Variance for the First Two Principal Components which are Derived from a Principal Component Analysis (PCA) Using the Residuals from Allometric PGLS Volume regressions of Several Brain Structures Vs. Telenecephalic Volume

Variable	PC1	PC2
Nidopallium	0.134	-0.043
Mesopallium	0.271	-0.099
Arcopallium	0.304	0.481
Striatum	0.247	0.064
Hyperpallium	-0.796	-0.207
Hippocampus	-0.350	0.842
Proportion of Variance	0.640	0.225

larger relative forebrains than would be expected from predictions based on their reference volume and compared to long-distance migrants. Further, migration distance predicts the first principal component (PC1) derived from nine 'non-invasive' brain measures including brain volume and forebrain hemispheric callipers (Figure **2B**). From telencephalic volume fractions and 3-D reconstructions, we can attribute the telencephalic expansion observed in SD species to pallial subregions that develop from the embryonic dorsal ventricular ridge [28], *i.e*. meso-, nido- and arcopallium. However, in contrast to DVR derived pallial regions, the 'dorsal cortex', *i.e*. hyperpallium or 'Wulst' and the hippocampus appear to be larger than predicted from allometric expectations in long-distance migrant birds and smaller than expected in SD birds (Figure **3D**). As the hyperpallium (including hyperpalliumdenso-cellulare) and hippocampus only account for about 15 % and the three DVR regions for 60 % of total telencephalon volume, the increase in dorsal cortex volume of LD animals cannot compensate for the overall reduced brain size in long-distance migrants.

The question arises whether the observed evolutionary differences in brain organization between migrants and non-migrants can be explained by differences in developmental mechanisms or by differences that emerge from specific behavioural adaptations that modify the same conserved, neurogenetic pattern in migrant and sedentary birds. A possible answer can be inferred by comparing the differences in telencephalic regionalization between migrants and non-migrants with recently found species differences in telencephalic neurogenesis. From such studies, it was found that 'large brained birds', such as parrots and passerines, enlarge their telencephalon by delaying the time at which telencephalic precursor cells exit the proliferative cell cycle [29]. Extending the period of neurogenesis seems to be the most effective mechanism to produce the observed differences in forebrain structures [30] because it implies an enlargement of 'late' structures ('late equals large' concept). A delay in the offset of neurogenesis causes location selective neurons to mature late, which in turn might conflict with the restricted 'ontogenetic window' available for migrants. For example, a comparison of moult duration and hatching date [31], as well as age of birds at the onset of migratory restlessness and hatching date, among African, European and Siberian stonechats clearly demonstrates shorter time frames available for maturation in the long distance (Siberian) migrants. Here we find that the volume of DVR derived subdivisions, specifically the meso- and nidopallium are enlarged in non-migrants and this enlargement correlates with brain size, as would be predicited by the 'late equals large' rule. These observations would indicate that long-distance migrants and shorter distance/-sedentary passerines may build on the same neurogenetic program, but they differ in the time available for brain differentiation. However, this view cannot explain the observed enlargement of the dorsal pallium in migrants. Yet there is another observation relevant to the present findings: the regionalization of an additional proliferative zone, adjacent to the ventricular zone (VZ) and referred to as the subventricular zone (SVZ), which has the capacity to increase the rate and expand the duration of neurogenesis [32]. The pallial distribution of the SVZ is confined to the ventricles associated with the DVR and is conspicuously absent from dorsal pallium (hyperpallium) in birds [33]. Generally, the SVZ gives rise to supra-granular neurons that are absent in the dorsal pallium of sauropsids, a finding that developmenttally further dissociates hyperpallial from DVR derived regions in the avian brain. In addition, a comparison between the large brain of parrots and the small brain of quail during different stages of development shows delayedtelencephalic development together with a distinct expansion of the DVR and subpallial SVZ in the developing parrot brains when compared to brains of quail. A preferential investment in the SVZ poolwhich line DVR regions in SD birds at the expense of VZ based neurogenesis whose cells end up in the dorsal pallium, could then explain the observed hyperpallial expansion in LD birds.

Taken together the above findings highlight developmental mechanisms that dissociate precisely

those regions in the avian forebrain that we find to be different between long-distance migrant and short-distance/ non-migrant passerine species and species populations. The open question of whether migrant and non-migrant species differ in the expansion, distribution and/or timing of an active SVZ during late stages of development remains to be answered.

A functional interpretation of the observed variation in structure size must take into acount the different roles attributed to the nuclear organization of DVR derived pallial regions and the 'semi-layered' hyperpallium. Rostral DVR functionally resembles the temporal neocortex in mammals [34], whereas the caudo-lateral nido-pallial (NCL) area constitutes a multimodal telencephalic region that functionally resembles the mammalian prefrontal cortex [3]. DVR regions, in particular the nidopallium, have been implicated in a number of higher order cognitive processes in birds including cognitive flexibility, innovation rate and tool making in crows [35]. All these functions seem to be well suited to cope with challenges associated with highly seasonal environments in sedentary birds. In contrast to the higher order processing characteristics of the DVR, the hyperpallium is characterized by a primary somatosensory region and a visual area that receives a direct, thalamically relayed retinal input along the thalamofugal path way (as opposed to the visual entopallium of the DVR, which receives indirect tectofugal information). High acuity retinotopic representations have been found to require a larger number of neurons, as was initially shown in primate area 17 of visual cortex [36]. As such, a larger relative hyperpallium could be of advantage in migratory behaviour.

Finally, migrant birds seem to host specialized functions in the visual hyperpallium such as sun-compass sensitive activities [37], night-vision and geomagnetic sensitive areas, *e.g*. cluster N [40]. Overall, compared to sedentary birds, a larger dorsal pallium in long-distance migrants, associated with a decrease in DVR derived telencephalization, is compatible with neurogenetic mechanisms, which organize the avian forebrain and the neural regionalization underlying behaviour.

The present findings elucidate a relation between brain geometry and function at the macroscopic level of telencephalic subdivisions in birds. At this organizational level, the functional correlates are likely to involve multiple and intercorrelatedselective traits, hierarchically constructed from a set of life-history variables as suggested recently [39]. We show that the migratory status of birds reflects one such life-history variable. We further provide evidence that the developmental mode, which leads to the observed differences, is the constraining and dynamical factor that determines this particular relationship between structure and function. A further refinement of specific volumetries could involve consideration of the recently demonstrated large scale network organization in the avian forebrain [40]. We expect that a mapping onto the cellular level, *i.e*. the avian forebrain connectome, would further disclose functional attributes underlying the relationship between forebrain geometry and population level behaviour.

ACKNOWLEDGEMENTS

We deeply acknowledge the technical assistance provided by Ilse Holzinger from the Neurosignaling Unit, Dept. of Organismic Biology, University of Salzburg. We are grateful to Barbara Helm from the MPI for Ornithology in Seewiesen/Andechs, Germany for her kind donation of birds. We further acknowledge and are grateful for the help of Al Kamil, Ross Dawkins, Elizabeth Keller and the Cedar Point Biological Station of the University of Nebraska for assisting in the field work carried out in the USA. We also forward special thanks to Francisco Valera and Wolfgang Vogl for field assistance in Spain and Austria. Special thanks are given to Carlos Illera for his sequence data of African stonechats. Finally we appreciate the funding provided by the J.P.ScottCenter for Neuroscience, Mind and Behavior at Bowling Green State University, USA.

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Received on 04-07-2014 Accepted on 21-07-2014 Published on 18-10-2014

http://dx.doi.org/10.15379/2409-3564.2014.01.01.1