Abstract

Brain processing capacity has traditionally been inferred from data on brain size. However, recent studies have shown that similarly sized brains of distantly related species can differ markedly in the number and distribution of neurons, their basic computational units. Therefore, a finer-grained approach is needed to reveal the evolutionary paths to increased cognitive capacity. This quantitative approach to the evolution of brain processing capacity at the cellular level is relatively new, since quick and reliable estimation of the number of neurons in whole brains or large brain regions has only become possible in the past 15 years or so with the introduction of the isotropic fractionator. This method of determining brain cellular composition is applicable to a wide range of questions. We can assess intraspecific variation, both at the individual and population level, examine the effect of sex and age, and the study selection at the intraspecific level. At the other side of the spectrum, we can study large macroevolutionary trends or try to isolate the effect of specific selective pressures by comparing more closely related and ecologically similar species. In this thesis, I explored variation in brain size and brain cellular composition across vertebrates at both intraspecies and interspecies level.

In Chapter 1, we showed that different populations of the Madagascar ground gecko can vary substantially in the number of brain neurons. There were no sex differences in brain size, number of neurons, or neuron density, even though the species is moderately sexually dimorphic. We also provided evidence that postnatal neurogenesis in geckos does not only replace lost neurons but adds new ones and that this is especially pronounced in the adult telencephalon.

In Chapter 2, we assessed the effect of artificial selection for large relative brain size in guppies on the numbers of neurons. We discovered that it leads to a corresponding increase in the number of neurons. Female guppies in the small-brained and large-brained groups did not differ in neuron density, so the larger brains translated linearly to an increase in neurons. This might explain a host of enhanced cognitive abilities previously described in the large-brained guppies.

In Chapter 3, we tested the social brain hypothesis by directly looking at neuron numbers for the first time. Using Bayesian phylogenetic generalized linear mixed models, we found no association between sociality and any measure of brain size or proxy of brain capa-

city, showing that sociality in and of itself does not necessarily lead to larger brains and intelligence. It seems that metabolic constraints and possibly increased hypoxia tolerance outweigh any potential benefits of higher brain processing capacity in this specific case and that the nature of social complexity (organisational vs. relational) might be an important factor.

Finally, in Chapter 4, we reconstructed the evolution of brain neuron numbers in amniotes. We analysed a dataset comprising brain sizes of almost 4000 species of amniotes and neuron numbers in three major brain parts of 251 species. We found that non-avian reptiles have rather low absolute numbers of neurons. Besides their low encephalization (brain size relative to body size), they also feature lower neuron densities, resulting in substantially fewer neurons per body mass compared to endotherms. This holds despite the fact that, across amniotes, neuron densities go down with increasing brain size. Using reversible jump MCMC, we were able to identify significant changes in neuron-brain scaling along amniote phylogeny, without any *a priori* hypotheses. We found that birds and mammals have independently increased not only brain size, but also neuron density, converging on a similar scaling relationship, while there were no significant shifts within non-avian reptiles over the span of 325 million years. This again highlights the importance of energetic constraints in brain evolution. Moreover, this difference between endotherms and ectotherms is most pronounced in the cerebellum, not in the telencephalon. Other two major increases in relative brain size and neuron density occurred in anthropoid primates and core landbirds (Telluraves), again resulting in similar scaling.