Developmental basis for telencephalon expansion in waterfowl: enlargement prior to neurogenesis

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Some altricial and some precocial species of birds have evolved enlarged telencephalons compared with other birds. Previous work has shown that finches and parakeets, two species that hatch in an immature (i.e. altricial) state, enlarged their telencephalon by delaying telencephalic neurogenesis. To determine whether species that hatch in a relatively mature (i.e. precocial) state also enlarged their telencephalon by delaying telencephalic neurogenesis, we examined brain development in geese, ducks, turkeys and chickens, which are all precocial. Whereas the telencephalon occupies less than 55 per cent of the brain in chickens and turkeys, it occupies more than 65 per cent in ducks and geese. To determine how these species differences in adult brain region proportions arise during development, we examined brain maturation (i.e. neurogenesis timing) and estimated telencephalon, tectum and medulla volumes from serial Nissl-stained sections in the four species. We found that incubation time predicts the timing of neurogenesis in all major brain regions and that the telencephalon is proportionally larger in ducks and geese before telencephalic neurogenesis begins. These findings demonstrate that the expansion of the telencephalon in ducks and geese is achieved by altering development prior to neurogenesis onset. Thus, precocial and altricial species evolved different developmental strategies to expand their telencephalon.

Keywords: neurogenesis; Anseriformes; size; telencephalon; precocial; altricial

1. INTRODUCTION

Parrots, songbirds and waterfowl (Anseriformes) have evolved an expanded telencephalon relative to chicken-like birds (Galliformes; Portmann 1947; Boire & Baron 1994; Iwaniuk & Hurd 2005). Parrots and songbirds were long thought to be distant relatives, but some molecular data suggest that these two avian orders may be closely related to one another (Ericson *et al.* 2006; Hackett *et al.* 2008). Waterfowl are the sister group of chicken-like birds, and both of these are distantly related to songbirds and parrots (Ericson *et al.* 2006; Hackett *et al.* 2008). Given these interrelationships, it is most parsimonious to conclude that expanded telencephalons evolved at least twice independently in birds: once in waterfowl and at least once in the group that includes songbirds and parrots. This raises an interesting question: did parrots, songbirds and waterfowl enlarge their telencephalon by means of similar developmental mechanisms?

Increased telencephalization in mammals results primarily from a general developmental mechanism that causes coordinated changes in most brain regions. Specifically, it has been shown that the proportional size of the telencephalon tends to increase predictably with overall brain size. As mammals evolved larger brains, developmental schedules were uniformly stretched

(Finlay & Darlington 1995; Clancy *et al.* 2001). Such uniform stretching causes brain structures that are born late in development, such as the telencephalon, to become disproportionately large relative to brain regions that are born earlier. A crucial aspect of this ‘concerted brain evolution’ is that neurogenesis timing is highly conserved.

Although mammalian brain regions tend to scale predictably with overall brain size, this is not always the case. Instances of ‘mosaic brain evolution’, in which brain regions expand independently of each other, have also been noted. For example, the telencephalon is larger in primates than insectivores, even after controlling for differences in absolute brain size (Stephan *et al.* 1981; Barton & Harvey 2000). Mosaic brain evolution is also common in birds (Iwaniuk *et al.* 2004). Parrots and songbirds, for example, have proportionally larger telencephalons than Galliformes, even when brain size is similar (Boire & Baron 1994). Likewise, the telencephalon is proportionally larger in Anseriformes than Galliformes even after controlling for differences in absolute brain size (Boire & Baron 1994).

The developmental mechanisms underlying such mosaic differences in brain region proportions have not been studied extensively. However, it has been shown that the proportional reduction of the limbic system in primates is associated with an advance in the timing of limbic system neurogenesis (Finlay *et al.* 1998; Clancy *et al.* 2001). It has also been noted that the expansion of the telencephalon is associated with the expansion of the neurogenetic subventricular zone (SVZ) within the

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primate telencephalon (Smart *et al.* 2002). Our own previous work showed that parakeets enlarged their telencephalon by delaying and extending telencephalic neurogenesis, expanding the telencephalic SVZ and delaying the decline in the rate at which telencephalic precursors cells cycle (Charvet & Striedter 2008; Striedter & Charvet 2008). Delayed telencephalic neurogenesis and SVZ expansion also account for the expansion of the telencephalon in songbirds (Charvet & Striedter 2009).

Because alterations in neurogenesis timing feature so prominently in these previous studies of mosaic brain evolution, one might expect that the expansion of the telencephalon of waterfowl is likewise associated with delays in telencephalic neurogenesis. However, in contrast to parrots and songbirds, waterfowl are precocial birds with hatchlings that follow their parents but are never fed by them (Starck & Ricklefs 1998). This precociality may have limited the ability of waterfowl to extend telencephalic neurogenesis into the post-hatching period. Therefore, we hypothesized that waterfowl might have enlarged their telencephalon by changing developmental parameters other than neurogenesis timing. Specifically, we considered that Anseriformes might have enlarged their telencephalon before neurogenesis begins.

To test our hypothesis, we compared brain development between two species of waterfowl, namely domestic ducks and geese (*Anas platyrhynchos domesticus* and *Anser anser domesticus*), and two chicken-like birds, namely domestic chickens and turkeys (*Gallus gallus domesticus* and *Meleagris gallopavo domesticus*). We quantified neurogenesis timing and the size of the telencephalon, the tectum and the medulla and asked when species differences in brain region proportions emerge. Our principal finding is that, after controlling for differences in incubation length, neurogenesis timing is highly conserved across these species. However, the telencephalon is larger in waterfowl than in chicken-like birds before telencephalic neurogenesis begins. This suggests that waterfowl probably expanded their telencephalon by changing the amount of territory allocated to the telencephalic fate at the time of brain regionalization (when the major brain regions become molecularly distinct). Combined with previous results, our data show that precocial and altricial species expanded their telencephalon by altering different developmental parameters.

2. MATERIAL AND METHODS

Nineteen duck (*A. platyrhynchos domesticus*), 11 goose (*A. anser domesticus*), 10 turkey (*M. gallopavo domesticus*) and 12 chicken (*G. gallus domesticus*) eggs were obtained from commercial suppliers. The eggs were incubated in a rotating egg incubator (Avey Incubators, model GB-1) at 37.8°C and 50–60% humidity. Specimens were collected between embryonic day (ED) 3–5 and ED 14. Embryos were removed from the egg, freed from extra-embryonic tissues, blotted dry, weighed on a precision balance and immersed in methacarn (60% methanol, 30% chloroform and 10% glacial acetic acid). For embryos older than ED 10, only heads were weighed and used for morphometric analysis. After fixation, embryos were stored in 70 per cent ethanol. Embryos were embedded in paraffin and sectioned serially at 20 µm. Most embryos were sectioned horizontally

and a few were sectioned transversely. The sections were stained with Giemsa (Sigma-Aldrich Inc.) and coverslipped.

(a) Analysis of brain region growth

To estimate the volume of several major brain regions, we mounted 29–65 regularly spaced sections through each specimen. Section spacing varied across specimens to account for differences in specimen size, but in each specimen, 15–30 sections spanned the brain. The mounted sections were photographed with a digital colour camera (Spot Insight, Diagnostic Instruments, Sterling Heights, MI, USA) attached to a macro lens or a light microscope (BH-2, Olympus, Center Valley, PA, USA) equipped with a low-power objective. Regions of interest were outlined in each section, and area measurements were made with the software package IMAGEJ (Rasband 1997–2007). The sum of each region's cross-sectional area was multiplied by the distance between sections. To correct for tissue shrinkage, we divided all volume estimates by an embryo-specific shrinkage factor, which was calculated by dividing each embryo's reconstructed body (or head) volume by the corresponding fresh body (or head) weight, divided by the fresh tissue's estimated specific gravity of 1.04 g cm⁻³ (Stephan *et al.* 1981). The procedures are identical to those we previously employed to study embryonic brain growth in parakeets (*Melopsittacus undulatus*) and bobwhite quail (*Colinus virginianus*; Striedter & Charvet 2008); we include the previously published quail data in some of the present analyses.

Our morphometric analysis is limited to a few major brain regions that are morphologically identifiable by ED 3–5. We delineated the telencephalon, optic tectum and the medulla, which was operationally defined as extending from the entrance of the trigeminal nerve to the beginning of the spinal cord. The remaining brain comprises mainly diencephalon, tegmentum and cerebellum. These delineations are identical to those we employed previously (Striedter & Charvet 2008; Charvet & Striedter 2009).

Volumetric comparisons were based on absolute region volumes, fractional region volumes (structure volume divided by total brain volume) and region volume relative to medulla volume. These measures were used because they are most useful for comparisons across ages and species, as evidenced by their extensive use in previous studies (Portmann 1947; Iwaniuk & Hurd 2005; Striedter & Charvet 2008).

(b) Analysis of neurogenesis timing

At early stages of development, the vertebrate brain consists of a ventricular zone (VZ) comprised of proliferating cells. As cells exit the cell cycle, they tend to exit the VZ and form a largely post-proliferative, less dense mantle zone (MZ). As the brain matures, the MZ expands. At intermediate stages of maturation, an SVZ emerges in the telencephalon. It is defined as a cell-dense zone containing adventricular mitoses, which can be detected in Nissl-stained material. Collectively, the VZ and the SVZ constitute the telencephalon's proliferative zone.

Proliferative and MZ areas were measured on low-magnification images from regularly spaced sections, relying on abrupt changes in cell density to define the boundaries between the zones. From these data, we calculated each region's proliferative zone fraction (PZF), defined as the sum of the proliferative zone areas (including the SVZ when it exists) divided by the total area of the proliferative

Figure 1. Photographs of (a) a chicken and (b) a duck at ED 5.75 (Hamburger–Hamilton stage 29, approx. 27% incubation) and ED 7 (Hamburger–Hamilton stage 28, approx. 27% incubation), respectively. These images show that the telencephalon (white lines) is larger in ducks compared with incubation-matched chickens. Scale bar, 1 mm.

and MZs. These PZFs indicate how much neurogenesis has occurred within a brain region. A PZF of 1 implies that neurogenesis has not yet begun. A PZF near 0 implies that neurogenesis is nearly complete. The embryos selected for this analysis cover the range of ages during which the MZ emerges and the VZ shrinks substantially. PZF curves were generated for the telencephalon, the tectum and the medulla. The remaining brain regions were not analysed, because they are more heterogeneous in terms of neurogenesis timing.

(c) Curve fitting and statistics

PZF curves were fitted with sigmoid functions using the software package IGOR PRO (Wavemetrics, Lake Oswego, OR, USA). Because the brain region growth curves exhibit more complex shapes, they were not fitted by simple functions. Instead, they are displayed as individual data points, overlaid with an interpolated curve obtained by applying a smoothing spline operation. Separate interpolated curves were obtained for the anseriform and galliform species. PZF data for bobwhite quail from a previous study using identical methods (Striedter & Charvet 2008) were included in this analysis. All smoothing parameters were adjusted visually, the main criterion being that the interpolated curves are smooth (have few inflection points) yet fit the data visually.

Statistical analyses were performed with the software package JMP (SAS, Cary, NC, USA). The PZF curves were compared across the species using a generalized linear model with a sigmoid fit. This analysis was based on data from six goose, 17 duck, nine turkey and 15 chicken embryos. Statistical comparison of growth curves was limited to very young embryos, up to and including 20 per cent of incubation. Therefore, this analysis was based on seven ducks, four geese, six chickens, two turkeys and one quail. Because differences between orders were much larger than differences between species within an order, we combined data from species in the same order. In other words, we compared 11 anseriform and 9 galliform embryos. As the

anseriform and galliform growth curves are both well fitted with straight lines over this range of ages and specimens, an analysis of covariance (ANCOVA) was performed to determine whether Anseriformes differed from Galliformes. Allowing for unequal slopes in the ANCOVAs did not impact the statistical significance of the results.

3. RESULTS

Embryologists often describe embryos in terms of their stage of maturity, typically identified by Hamburger and Hamilton's criteria (figure 1; Hamburger & Hamilton 1951). Unfortunately, such descriptions yield a discontinuous time axis unsuitable for the construction of growth curves. Alternately, one might describe an embryo in terms of the number of days the embryo was incubated. When we constructed PZF curves on the basis of such an absolute time axis (figure 2a), it becomes obvious that chicken embryos mature faster than turkeys and bobwhite quail. However, this difference in maturation rate largely disappears when we employ a third type of time axis (figure 2b), namely per cent of incubation (i.e. each individual's absolute age, multiplied by 100 and divided by each species' average incubation period in days). A statistical analysis of the telencephalic PZF data confirms that a significant species effect exists if absolute age is used as the time axis (general linear model: d.f. = 3; $\chi^2 = 51.4$; $p < 0.001$), but not if the PZF data are correlated against per cent of incubation (d.f. = 3; $\chi^2 = 7.45$; $p > 0.05$).

Further analysis of the PZF data shows that neurogenesis timing is conserved across species not only in the telencephalon (figure 2a,b) but also in the medulla and optic tectum (figure 2c,d). The medulla matures early and quickly, starting neurogenesis at approximately 16 per cent of incubation and is nearly complete by 30 per cent. The tectum begins neurogenesis later, approximately 27–28% of incubation and is nearly complete by 40 per cent of incubation. The telencephalon

Figure 2. Analysis of the PZF data shows that neurogenesis timing is highly conserved across waterfowl (Anseriformes) and chicken-like species (Galliformes) once age is expressed in terms of per cent incubation. (a) A plot of telencephalic PZFs versus age in days shows that the telencephalon matures earlier in chickens than in other chicken-like birds or waterfowl. In contrast, if PZFs are plotted against per cent incubation, then tissue maturation becomes highly predictable for the (b) telencephalon, (c) the tectum and (d) the medulla. Hatching typically occurs after 30, 28, 26 and 21 days of incubation in geese, turkeys, ducks and chickens, respectively. Open circle, goose; filled circle, duck; open diamond, turkey; filled diamond, chicken.

begins neurogenesis at approximately the same time as the medulla (17–20% of incubation) but ceases around the same time as the optic tectum. Thus, the period of telencephalic neurogenesis is protracted compared with that of the medulla or the tectum.

The size of the SVZ, which is included in the calculation of the telencephalic PZF curves, is similar in Anseriformes and Galliformes. In both orders, a telencephalic SVZ emerges by 23 per cent of incubation and fades by 53 per cent of incubation.

Examination of the volumetric growth curves for individual brain regions reveals that chicken brains grow more quickly than those of the other species in our dataset if absolute time is used as a time base (figure 3a; data for other regions not shown). In contrast, if per cent incubation is used as the time base, then the chicken, turkey and quail curves become closely aligned. This is shown for the telencephalon in figure 3b, but is also true for the tectum and the medulla (figure 4a,b). Importantly, the use of per cent incubation as a time axis reveals that the telencephalon growth curves differ between Galliformes and Anseriformes. In terms of absolute volume, the telencephalon is 2.5–4 times larger in Anseriformes than in Galliformes until approximately 45 per cent of incubation is completed (figure 3b). If telencephalon volume is expressed relative to overall brain size (i.e.

fractional telencephalon volume; figure 3c), then the telencephalon is approximately 50 per cent larger in Anseriformes than in Galliformes. A similar species difference is evident also if telencephalon volume is expressed relative to medulla volume (i.e. telencephalon/medulla ratio; figure 3d).

These results suggest that the telencephalon is larger in Anseriformes than in Galliformes before telencephalic neurogenesis begins in earnest; that is, before approximately 20 per cent of incubation is complete. To confirm this statistically, we selected all embryos less than or equal to 20 per cent of incubation, pooled data within orders and subjected it to ANCOVAs, using per cent incubation as the time base ($n = 11$ Anseriformes and 9 Galliformes). The differences between orders were significant for absolute telencephalon volume ($t = 4.65$; $p < 0.01$), fractional telencephalon volume ($t = 4.3$; $p < 0.01$) and telencephalon/medulla ratio ($t = 3.21$; $p < 0.01$). In contrast, no significant taxonomic order effects were seen in the equivalent ANCOVAs for absolute tectum ($t = 0.82$; $p > 0.05$) or medulla volume ($t = 2.13$, $p > 0.05$; figure 4a,b). A significant order effect was observed for proportional tectum volume ($t = -8.7$; $p < 0.01$; figure 4c), but not for the tectum/medulla ratio ($t = -1.86$; $p > 0.05$; figure 4d). These results suggest that proportional tectum size is smaller in Anseriformes

Figure 3. Brain region growth curves reveal that the telencephalon is larger in waterfowl (Anseriformes) than in incubation-matched chicken-like birds (Galliformes). (a) If absolute telencephalon volume is plotted against age in days, then the telencephalon seems to grow faster in chickens (filled diamond) than in turkeys (open diamond), quail (diamond with a dot), geese (open circle) or ducks (filled circle). (b) However, if telencephalon volume is plotted against age expressed as per cent of the incubation period, then the telencephalon is consistently larger in Anseriformes than in Galliformes. (c) Similarly, telencephalon size relative to overall brain size (i.e. fractional telencephalon volume) is consistently larger in Anseriformes than in incubation-matched Galliformes. (d) The size of the telencephalon relative to the medulla is likewise larger in Anseriformes than in Galliformes, at least until approximately 40 per cent incubation. Volumetric measurements of the brain of bobwhite quail are from an earlier study that used identical methods (Striedter & Charvet 2008).

than in Galliformes not because the former have a smaller tectum (relative to the medulla or in absolute terms) but because they have a larger telencephalon.

4. DISCUSSION

The proportional size of the telencephalon in Anseriformes (ducks and geese) rivals that in parrots and songbirds (Burish *et al.* 2004). However, the developmental mechanisms responsible for the expansion of the telencephalon in anseriform birds differ from those in songbirds and parrots. In songbirds and parrots, telencephalic neurogenesis, as determined from PZF curves, is delayed relative to the medulla and relative to telencephalic neurogenesis in Galliformes (Striedter & Charvet

2008; Charvet & Striedter 2009). Therefore, the expansion of the telencephalon in parrots and songbirds does not appear until relatively late in embryonic development. In contrast, we here show that the Anseriformes have not delayed telencephalic neurogenesis. Instead, they have enlarged their telencephalon at very early stages of development.

The early expansion of the telencephalon in Anseriformes might arise because telencephalic precursor cells cycle faster in Anseriformes than in Galliformes. We have no direct evidence for or against this hypothesis. However, the slopes of the growth curves for absolute telencephalon volume are similar in Anseriformes and Galliformes, once controlled for the differences in incubation period (figure 2b). Therefore, if Anseriformes

Figure 4. (a) The absolute volume of the tectum is similar in waterfowl (Anseriformes) and incubation-matched chicken-like birds (Galliformes), but (b) the medulla is slightly larger in the waterfowl. (c) The tectum's volume fraction is smaller in waterfowl than in chicken-like birds, but (d) the tectum/medulla ratio is similar in the two orders until approximately 30 per cent of incubation. Thereafter, the tectum/medulla ratio is larger in chicken-like birds. The data for bobwhite quail (*C. virginianus*) are from Striedter & Charvet (2008). Filled circle, duck; open circle, goose; filled diamond, chicken; open diamond, turkey; diamond with a dot, quail.

enlarged their telencephalon by increasing the telencephalic cell cycle rate, this increase would be limited to extremely early stages of telencephalic development. Alternatively, the expansion of the telencephalon in Anseriformes could be due to alterations in gene expression at the time of brain regionalization. We have previously hypothesized that such a change in brain regionalization accounts for the enlargement of the tectum in Galliformes versus parrots (Striedter & Charvet 2008; Charvet & Striedter 2009). Of course, telencephalic enlargement in Anseriformes could be due to changes in both brain regionalization and local proliferation rates. Indeed, the combination of altered gene expression and local proliferation rates appears to account for the enlargement of the hypothalamus in blind cavefish versus their sighted relatives (Menuet *et al.* 2007).

To explain why Anseriformes, parrots and songbirds employed different developmental strategies to expand

their telencephalon, one may consider that Anseriformes are precocial, whereas parrots and songbirds are altricial species. We hypothesize that precocial birds may not be able to extend telencephalic neurogenesis into the post-hatching period, as songbirds and parrots can, because anseriform hatchlings must fend for themselves soon after hatching. This is not to say, however, that all altricial species must enlarge their telencephalon by delaying neurogenesis. It is not known, for example, whether woodpeckers and owls, which are altricial as well as highly telencephalized (Burish *et al.* 2004), enlarged their telencephalon by delaying telencephalic neurogenesis or by altering parameters other than neurogenesis timing. The main conclusion from our present work is that evolution has employed different developmental mechanisms to enlarge the telencephalon in different lineages. The functional correlates of these different developmental strategies remain to be studied.

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