Birds have primate-like numbers of neurons in the forebrain

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Some birds achieve primate-like levels of cognition, even though their brains tend to be much smaller in absolute size. This poses a fundamental problem in comparative and computational neuroscience, because small brains are expected to have a lower information-processing capacity. Using the isotropic fractionator to determine numbers of neurons in specific brain regions, here we show that the brains of parrots and songbirds contain on average twice as many neurons as primate brains of the same mass, indicating that avian brains have higher neuron packing densities than mammalian brains. Additionally, corvids and parrots have much higher proportions of brain neurons located in the pallial telencephalon compared with primates or other mammals and birds. Thus, large-brained parrots and corvids have forebrain neuron counts equal to or greater than primates with much larger brains. We suggest that the large numbers of neurons concentrated in high densities in the telencephalon substantially contribute to the neural basis of avian intelligence.

intelligence | evolution | brain size | number of neurons | birds

Many birds have cognitive abilities that match or surpass those of mammals (1). Corvids and parrots appear to be cognitively superior to other birds, rivalling great apes in many psychological domains (1–3). They manufacture and use tools (4, 5), solve problems insightfully (6), make inferences about causal mechanisms (7), recognize themselves in a mirror (8), plan for future needs (9), and use their own experience to anticipate future behavior of conspecifics (10) or even humans (11), to mention just a few striking abilities. In addition, parrots and songbirds (including corvids) share with humans and a few other animal groups a rare capacity for vocal learning (12), and parrots can learn words and use them to communicate with humans (13).

Superficially, the architecture of the avian brain appears very different from that of mammals, but recent work demonstrates that, despite a lack of layered neocortex, large areas of the avian forebrain are homologous to mammalian cortex (14–16), conform to the same organizational principles (15, 17, 18), and play similar roles in higher cognitive functions (14, 19), including executive control (20, 21). However, bird brains are small and the computational mechanisms enabling corvids and parrots to achieve ape-like intelligence with much smaller brains remain unclear. The notion that higher encephalization (relative brain size deviation from brain–body allometry) endows species with improved cognitive abilities has recently been challenged by data suggesting that intelligence instead depends on the absolute number of cerebral neurons and their connections (22–25). This is in line with recent findings that absolute rather than relative brain size is the best predictor of cognitive capacity (26–28). However, although corvids and parrots feature encephalization comparable to that of monkeys and apes, their absolute brain size remains small (29, 30). The largest average brain size in corvids and parrots does not exceed 15.4 g found in the common raven (29) and 24.7 g found in the hyacinth macaw (30), respectively. Do corvids and parrots provide a strong case for reviving encephalization as a valid measure of brain functional

capacity? Not necessarily: it has recently been discovered that the relationship between brain mass and number of brain neurons differs starkly between mammalian clades (31). Avian brains seem to consist of small, tightly packed neurons, and it is thus possible that they can accommodate numbers of neurons that are comparable to those found in the much larger primate brains. However, to date, no quantitative data have been available to test this hypothesis.

Here, we analyze how numbers of neurons compare across birds and mammals (32–39) of equivalent brain mass, and determine the cellular scaling rules for brains of songbirds and parrots. Using the isotropic fractionator (40), we estimated the total numbers of neuronal and nonneuronal cells in the cerebral hemispheres, cerebellum, diencephalon, tectum, and brainstem in a sample of 11 parrot species, 13 vocal learning songbird species (including 6 corvids), and 4 additional model species representing other avian clades (Figs. S1 and S2). Because most of the cited mammalian studies analyzed cellular composition of only three brain subdivisions, namely the pallium (referred to as the cerebral cortex in those papers), the cerebellum, and rest of brain, we divided the avian brain identically to ensure an accurate comparison of neuronal numbers, densities, and relative distribution of neurons in birds and mammals. Specifically, the avian pallium (comprising the hyperpallium, mesopallium, nidopallium, arcopallium, and hippocampus) was compared with its homolog—the mammalian pallium (comprising the neocortex, hippocampus, olfactory cortices such as piriform and entorhinal cortex, and pallial

Significance

Birds are remarkably intelligent, although their brains are small. Corvids and some parrots are capable of cognitive feats comparable to those of great apes. How do birds achieve impressive cognitive prowess with walnut-sized brains? We investigated the cellular composition of the brains of 28 avian species, uncovering a straightforward solution to the puzzle: brains of songbirds and parrots contain very large numbers of neurons, at neuronal densities considerably exceeding those found in mammals. Because these "extra" neurons are predominantly located in the forebrain, large parrots and corvids have the same or greater forebrain neuron counts as monkeys with much larger brains. Avian brains thus have the potential to provide much higher "cognitive power" per unit mass than do mammalian brains.
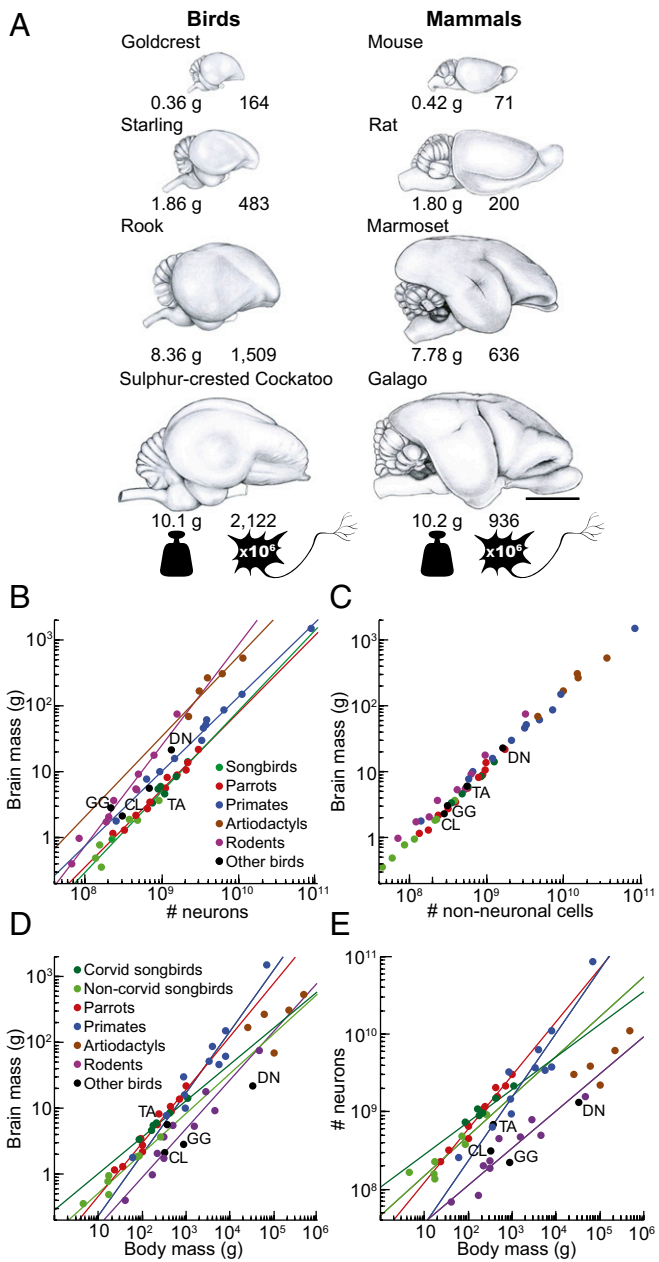
NEUROSCIENCE

Fig. 1. Cellular scaling rules for brains of songbirds and parrots compared with those for mammals. (*A*) Avian and mammalian brains depicted at the same scale. Numbers under each brain represent brain mass (in grams) and total number of brain neurons (in millions). Notice that brains of songbirds (goldcrest, starling, and rook) and parrots (cockatoo) contain more than twice as many neurons as rodent (mouse and rat) and primate (marmoset and galago) brains of similar size. (Scale bar: 10 mm.) (*B*) Brain mass plotted as a function of total number of neurons. Note that allometric lines for songbirds (green line) and parrots (red line) do not differ from each other, but they do differ from allometric lines for mammals (for statistics, see *SI Results*). (*C*) Brain mass plotted as a function of total number of nonneuronal cells. (*D*) Brain mass plotted as a function of body mass. (*E*) Total number of brain neurons plotted as a function of body mass. Allometric lines for the taxa examined are significantly different (for statistics, see *SI Results*). Each point represents the average values for one species. Data points representing noncorvid songbirds are light green, and data points representing corvid songbirds are dark green. The fitted lines represent reduced major axis (RMA) regressions and are shown only for correlations that are significant [coefficient of determination (r^2) ranges between 0.831 and 0.997; $P \leq 0.021$ in all cases]. Because nonneuronal scaling rules are very similar across the clades analyzed, the regression lines are omitted in *C*. Data for mammals are from published reports (for details, see *Methods*). CL, pigeon (*Columba livia*); DN, emu (*Dromaius novaehollandiae*); GG, red junglefowl (*Gallus gallus*); TA, barn owl (*Tyto alba*).

amygdala) (14–16, 41). The avian subpallium (formed by the striatum, pallidum, and septum), diencephalon, tectum, and brainstem were pooled and compared with the same regions of mammalian brains that are referred to as "the rest of brain." The cerebellum is directly compared between the two clades. The results of our study reveal that avian brains contain many more pallial neurons than equivalently sized mammalian brains.

Results

Total Numbers of Neurons. We found that the bird brains have more neurons than mammalian brains and even primate brains of similar mass (Fig. 1 *A* and *B*), and have very high neuronal densities (Fig. 2 *B* and *C*). Among the songbirds studied, weighing between 4.5 and 1,070 g, brain mass ranges from 0.36 to 14.13 g, and total numbers of neurons in the brain from 136 million to 2.17 billion (Fig. S3 and Table S1; for complete data see Datasets S1 and S2). In the parrots studied, body mass ranges between 23 and 1,008 g, brain mass from 1.15 to 20.73 g, and numbers of brain neurons from 227 million to 3.14 billion. Interestingly, the relationship between brain mass and the number of brain neurons can be described by similar power functions in these two bird
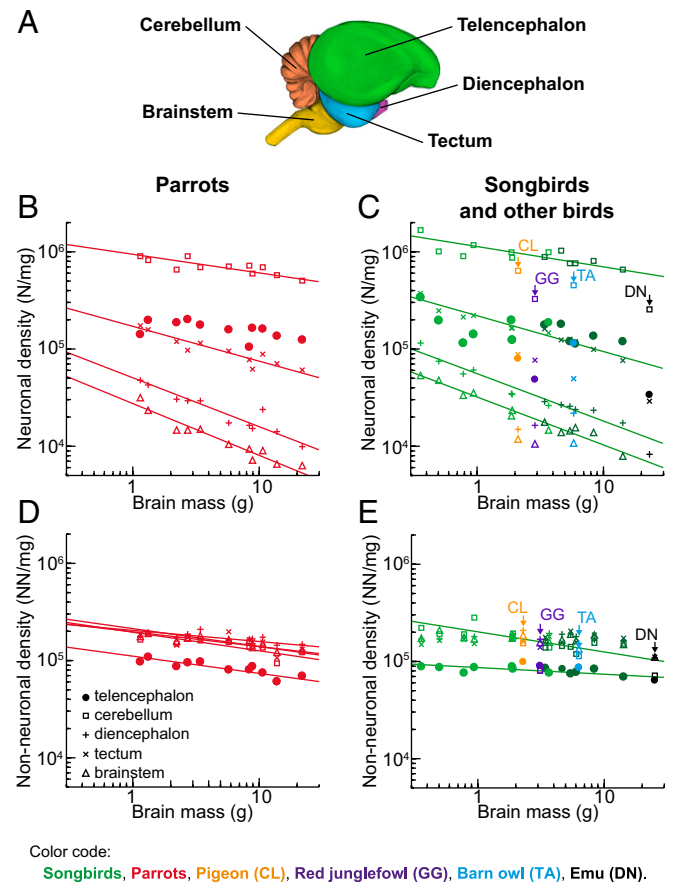

Fig. 2. Cellular densities in avian brains. (*A*) Lateral view of the starling brain showing the brain regions analyzed (for details, see *SI Methods* and Fig. S2). Neuronal (*B* and *C*) and nonneuronal cell density (*D* and *E*) plotted as a function of brain mass. Data points representing noncorvid songbirds are light green, and data points representing corvid songbirds are dark green. All graphs are plotted using the same *y*-axis scale for comparison. Note that neuronal density varies greatly among principal brain divisions and decreases significantly with increasing brain mass in all divisions but the telencephalon, whereas nonneuronal cell density is similar across brain divisions and species, but lower in the telencephalon (for statistics, see *SI Results*). The fitted lines represent RMA regressions and are shown only for correlations that are significant (r^2 ranges between 0.410 and 0.962; $P \leq 0.030$ in all cases).

Pallium **Cerebellum** **Rest of brain**

A — Songbirds, Parrots, Primates, Artiodactyls, Rodents (Neuronal density (N/mg) vs Pallium/Cerebral cortex mass (g); CL, TA, GG, DN)

B — Neuronal density (N/mg) vs Cerebellum mass (g); CL, TA, GG, DN

C — Neuronal density (N/mg) vs Rest of brain mass (g); CL, GG, TA, DN

D — % of brain neurons vs Brain mass (g); TA, GG, DN, CL

E — % of brain neurons vs Brain mass (g); CL, GG, DN, TA

F — % of brain neurons vs Brain mass (g); GG, CL, TA, DN

G — Eurasian Jay, Owl Monkey, Raven, Capuchin Monkey, Blue-and-yellow Macaw, Macaque monkey
# of neurons: 2.85 g / 529; 10.62 g / 442; 10.20 g / 1,204; 39.18 g / 1,140; 14.38 g / 1,917; 69.83 g / 1,710
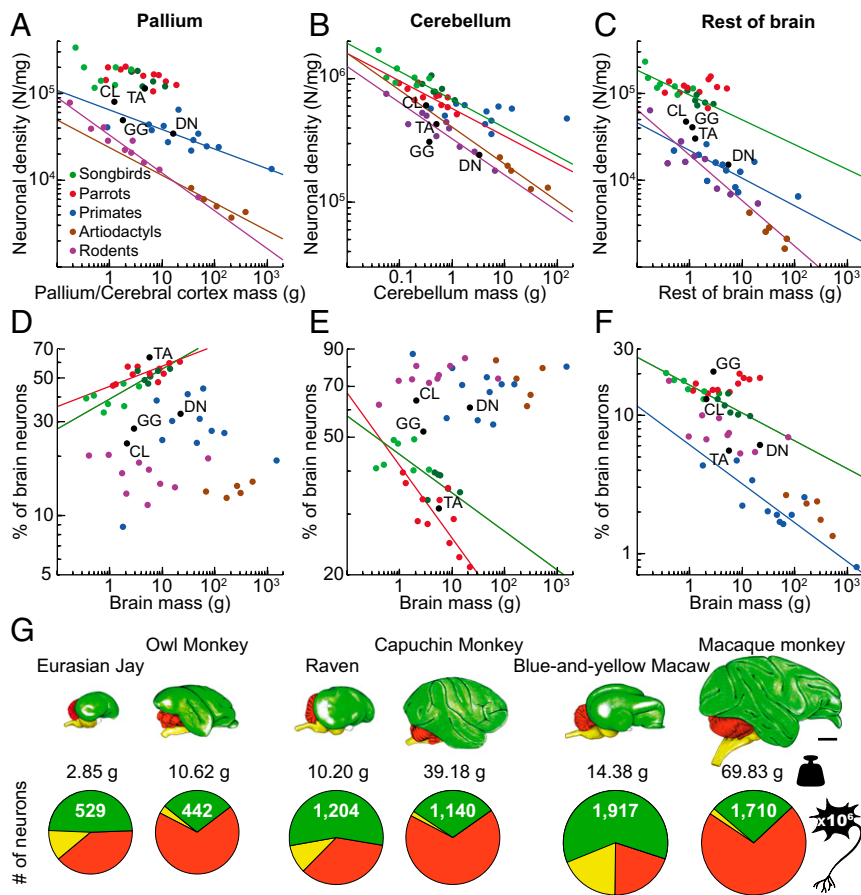
Fig. 3. Neuronal densities and relative distribution of neurons in birds and mammals. (A–C) Neuronal densities in the pallium (A), cerebellum (B), and rest of the brain (C). Note that neuronal densities are higher in parrots and songbirds than in mammals (for statistics, see *SI Results*). (D–F) Average proportions of neurons contained in the pallium (D), cerebellum (E), and rest of the brain (F). Note that increasing proportions of brain neurons in the rest of the brain in parrots are attributable specifically to increasing numbers of neurons in the subpallium (Fig. 5). Data points representing noncorvid songbirds are light green, and data points representing corvid songbirds are dark green. The fitted lines represent RMA regressions and are shown only for correlations that are significant (r^2 ranges between 0.389 and 0.956; $P \leq$ 0.033 in all cases). (G) Brains of corvids (jay and raven), parrots (macaw), and primates (monkeys) are drawn at the same scale. Numbers under each brain represent mass of the pallium (in grams) and total numbers of pallial/cortical neurons (in millions). Circular graphs show proportions of neurons contained in the pallium (green), cerebellum (red), and rest of the brain (yellow). Notice that brains of these highly intelligent birds harbor absolute numbers of neurons that are comparable, or even larger than those of primates with much larger brains. (Scale bar: 10 mm.) Data for mammals are from published reports (for details, see *Methods*). CL, pigeon; DN, emu; GG, red junglefowl; TA, barn owl.

groups (Table S2). Thus, songbirds and parrots with similar brain masses also have similar total numbers of brain neurons, as shown in Fig. 1B. Because the scaling exponents are significantly higher than 1.0 in both groups, any gain in number of brain neurons is accompanied by an even more pronounced gain of mass: a 10-fold increase in the number of brain neurons results in a 16.9- and 14.0-fold larger brain in songbirds and parrots, respectively. With their higher neuronal densities (Fig. 3 A–C), songbird and parrot brains accommodate about twice as many neurons as primate brains of the same mass and two to four times more neurons than rodent brains of equivalent mass (Fig. 1B). Songbirds and parrots also show a large brain mass for their body mass compared with nonprimate mammals (Fig. S4 A and B). Consequently, they have many more neurons than a nonprimate mammal of the same body size (Fig. 1E). For instance, the goldcrest's body mass is ~9-fold smaller than the mouse, but its brain has ~2.3-fold more neurons. Large corvids and parrots possess the largest avian brains, harboring the highest absolute numbers of neurons (Fig. 1 D and E and Fig. S4C). Their total numbers of neurons are comparable to those of small monkeys or much larger ungulates (Fig. S5).

Relative Distribution of Mass and Neurons. The bird/mammal comparison becomes even more striking when the relative distribution of neurons among the major brain components is taken into consideration. In the birds examined, the telencephalon mass fraction increases with brain size at the expense of all other brain components, ranging from 63% to 80% in songbirds, and from 71% to 85% in parrots (Fig. 4 A and B and Table S3); the relative proportion of the telencephalon resembles that reported for primates (42) (primates, 74 ± 5%; songbirds, 72 ± 6%; parrots, 78 ± 5%). The cerebellar mass fraction decreases from 11% to 8% in songbirds, and from 11% to 6% in parrots. Besides this, telencephalon mass scales approximately isometrically with the

number of neurons, whereas all other brain components hyper-scale in mass as they gain neurons (Table S2), because neuronal densities decrease and average neuronal sizes increase significantly as brains get larger within all brain parts but the telencephalon (Fig. 2 B and C). Thus, in contrast to mammals, larger brains of songbirds and parrots contain increasing proportions of neurons in the telencephalon, and correspondingly decreasing proportions of brain neurons in the cerebellum and other brain regions (Fig. 4 C and D). Neuronal densities in the avian pallium exceed those observed in the primate pallium by a factor of 3–4 (Fig. 3A). Hence, the telencephalon houses 38–62% of all brain neurons in songbirds and 53–78% in parrots (Fig. 4C); the pallium houses 33–55% in songbirds and 46–61% in parrots (Fig. 3D and Table S4). This markedly contrasts with the situation found in mammals, in which the pallium accounts for most of total brain volume, but the cerebellum houses a large majority of brain neurons (32–39) (Fig. 3 D–F). Notably, the human pallium contains a mere 19% of brain neurons but represents 82% of brain mass (38). Thus, when avian and mammalian brains of equivalent size are compared, avian pallial neurons greatly outnumber those observed in the mammalian pallium (Fig. 3G and Fig. S5). For instance, the goldcrest has ~64 million pallial neurons, almost five times more than the mouse pallium. The raven or the kea have ~1.2 billion pallial neurons, more than in the pallium of a capuchin monkey, and the blue-and-yellow macaw has ~1.9 billion pallial neurons, more than in the pallium of a rhesus monkey.

Subpallium. Although once believed to constitute almost the entire avian telencephalon (14), the subpallium (basal ganglia homolog) accounts only for 10–22% of total telencephalon volume in songbirds and for 15–18% in parrots, and houses only 9–16% of telencephalic neurons in songbirds and 14–24% in parrots (Tables S3 and S4). In songbirds, both the relative mass of the subpallium and the fraction of telencephalic
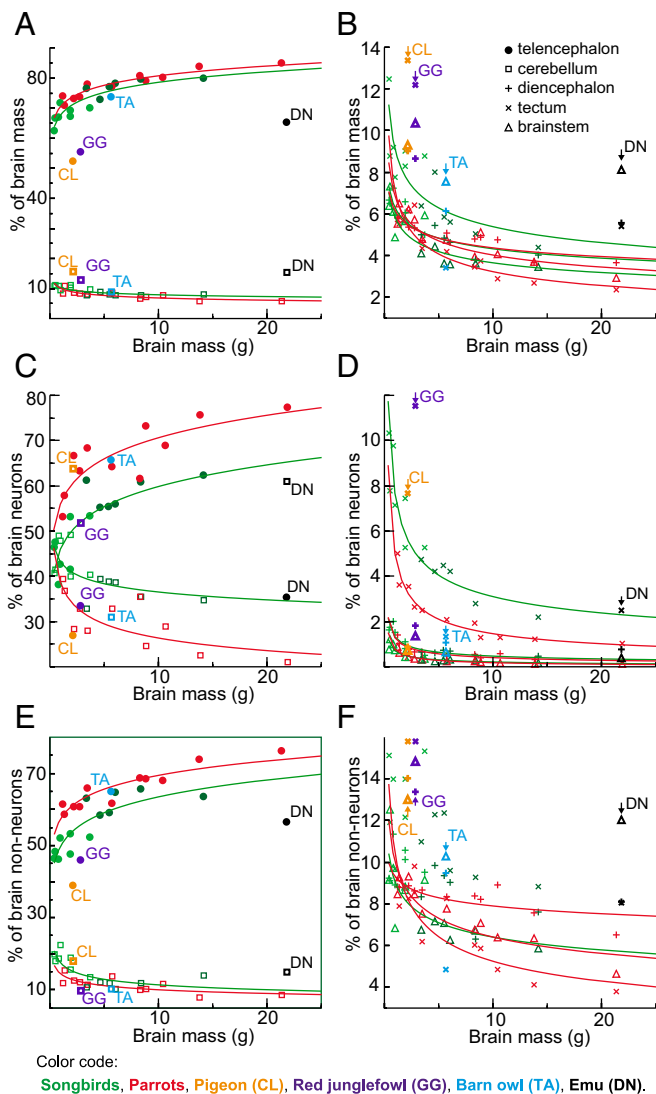
Fig. 4. Relative distribution of mass and cells in avian brains. Average percentages of mass (*A* and *B*), number of neurons (*C* and *D*), and number of nonneuronal cells (*E* and *F*) contained in the principal brain divisions relative to the whole brain in each species, plotted against brain mass. Data points representing noncorvid songbirds are light green, and data points representing corvid songbirds are dark green. The fitted lines represent RMA regressions and are shown only for correlations that are significant (r^2 ranges between 0.389 and 0.956; $P \leq 0.023$ in all cases). Note that both telencephalon mass fraction and proportions of neuronal and nonneuronal cells contained in the telencephalon increase with brain size.

Color code:
Songbirds, **Parrots**, **Pigeon (CL)**, **Red junglefowl (GG)**, **Barn owl (TA)**, **Emu (DN)**.

neurons contained within it decrease with increasing telencephalon size (Fig. 5 *B* and *C*). In parrots, in contrast, the relative mass remains constant and neuronal fraction increases with telencephalon size. Therefore, large-brained parrots have a relatively larger subpallium within the telencephalon that accommodates relatively more telencephalic neurons than that of large-brained songbirds (Fig. 5 *B*–*D*), implying that parrots have evolved a specific, previously unrecognized cerebrotype (43) distinguished by a higher number of neurons allocated to the subpallium. Because subpallial structures play an important role in sensory and motor learning and execution of motor behavior (15, 44), we suggest that the relatively enlarged subpallium in large parrots is likely associated with their greater learning skills, including vocal learning, and enhanced foot and beak dexterity (5, 6, 13, 45).

Nonneuronal Scaling Rules. Although neuronal scaling rules for avian brains differ from those for mammalian brains (Fig. 1*B*), nonneuronal scaling rules are shared between the two vertebrate classes (Fig. 1*C* and Table S2). In line with data from all mammals analyzed so far (32–39), the densities of nonneuronal (glial and endothelial) cells remain similar across bird species in all brain structures, except for the telencephalon, where nonneuronal cell density appears to be distinctively lower (Fig. 2 *D* and *E*). The latter may be a specific avian feature, as it has not been observed in mammals (31).

Glia/Neuron Ratio. Neurons outnumber nonneuronal cells in both bird groups examined (Fig. S6*A* and Table S5). The proportion of nonneuronal cells in the brain ranges between 21% and 37% in songbirds and from 31% to 41% in parrots. Hence, the maximal glia/neuron ratio (if all nonneuronal cells were glial cells) for the whole brain ranges from 0.27 to 0.59 in songbirds and from 0.44 to 0.69 in parrots. Like in mammals (32–39, 46), the proportion of nonneuronal cells is very small in the cerebellum, varying between 12% and 19% in songbirds and between 14% and 19% in parrots, but, in contrast to mammals, nonneuronal cells also constitute a minor cellular fraction in the telencephalon, representing 21–40% of cells in songbirds and 31–43% of cells in parrots (Fig. S6*B*). Nonneuronal cells predominate in the remaining brain regions analyzed, representing in songbirds and parrots, respectively, 60–90% and 79–94% of all cells in the diencephalon, 28–70% and 52–71% of all cells in the tectum, and 76–95% and 85–95% of all cells in the brainstem (Fig. S6*B*). The fact that neurons constitute an extremely small cellular fraction in the diencephalon of many avian species is an unexpected finding. Given that nonneuronal cell densities are similar to those found in most other brain divisions investigated (Fig. 2 *D* and *E*), this is unlikely to be due to a technical error. The numeric preponderance of neurons over nonneuronal cells in the bird brain as a whole is therefore due to the disproportionately large numbers of neurons in the telencephalon and cerebellum.

Corvid Brain as a Scaled-Up Songbird Brain. When considering the numbers of neurons and nonneuronal cells and their allocations to the major brain divisions, the same scaling rules apply to the brains of corvids and noncorvid songbirds (Figs. 1–5 and Table S2). Thus, it is not cellular composition but encephalization that sets corvids apart from other songbirds. Technically, residual brain mass calculated from regressions for all songbirds is significantly larger in corvids than in noncorvid songbirds [species examined in this study: $t_{(2,11)} = 2.542$, $P = 0.03$, Fig. 1*D*; species collated from literature: $t_{(2,848)} = 7.55$, $P < 10^{-6}$, Fig. S4*C*]. Because corvid brains tend to be larger than brains of noncorvid songbirds for any given body size (Fig. 1*D* and Fig. S4*C*), corvids have larger total numbers of neurons than noncorvid songbirds of the same body size (Fig. 1*E*). We suggest that corvid brains are scaled-up songbird brains, just as humans brains are to brains of nonhuman primates (38, 47), and that large absolute numbers of neurons endow corvids with superior cognitive abilities.

Comparison with Other Birds. The similarity of neuronal scaling rules between songbirds and parrots is not too surprising, considering their close phylogenetic relationship (48–51). The examination of outgroup taxa, however, suggests that, as in mammals (31), different neuronal scaling rules apply to various bird lineages. The closest relative to songbirds and parrots of the species sampled, the barn owl (Fig. S1) (48–51) resembles songbirds and parrots in terms of encephalization (Fig. 1*D*), relative telencephalon size (Fig. 4*A*), and neuronal densities in the telencephalon and diencephalon (Fig. 2*C*), but has a proportionally smaller subpallium (Fig. 5*B*) and lower neuronal densities in the tectum and cerebellum (Fig. 2*C*). The emu, the red junglefowl, and the pigeon, all species representing more basal bird lineages (Fig. S1), share lower degree of encephalization (Fig. 1*D*), a proportionally smaller telencephalon (Fig. 4*A*), small telencephalic and dominant cerebellar neuronal fractions (Fig. 4*C*), generally lower neuronal densities (Fig. 2*C*), and larger glia/neuron ratios (Fig. S6).
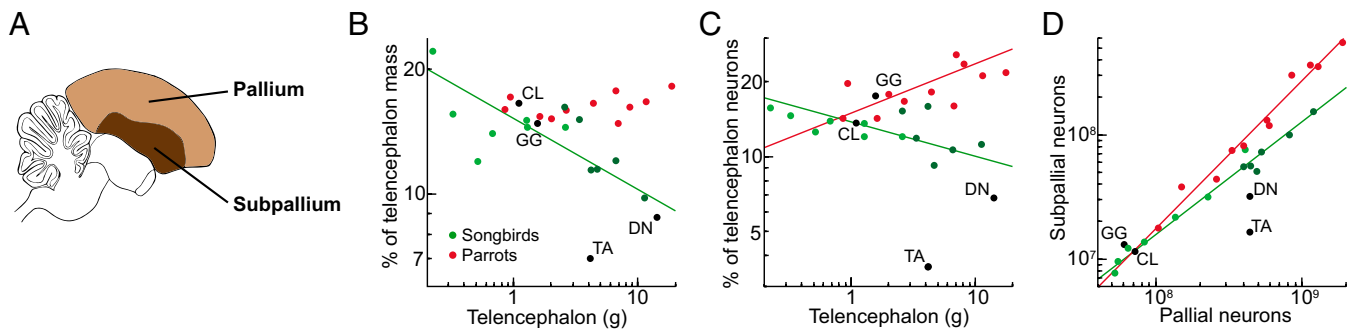
Fig. 5. Subpallium in avian telencephalon. (*A*) Diagram of sagittal section through the zebra finch brain showing relative position and size of the pallium and subpallium. (*B* and *C*) Average percentages of mass (*B*), number of neurons (*C*) contained in the subpallium relative to the whole telencephalon in each species, plotted against telencephalon mass. (*D*) Relationship between numbers of subpallial and pallial neurons. Note that, in parrots, the number of neurons in the subpallium increases faster than in the pallium (scaling exponent = 1.19 ± 0.13), whereas an opposite trend is observed in songbirds (scaling exponent = 0.91 ± 0.1). The fitted lines represent RMA regressions and are shown only for correlations that are significant (r^2 ranges between 0.379 and 0.981; $P \leq 0.025$ in all cases). Songbirds shown in green (data points representing noncorvids are light green, and data points representing corvids are dark green), parrots in red, and other birds in black. CL, pigeon; DN, emu; GG, red junglefowl; TA, barn owl.

Therefore, their brains harbor much smaller absolute numbers of neurons than brains of equivalently sized songbirds or parrots. For instance, although a red junglefowl is ~50-fold heavier than a great tit, both birds have approximately the same number of brain neurons (Fig. 1*E* and Fig. S3). Remarkably, even in these basal birds, neuronal densities in the pallium are still comparable to those observed in the primate cortex (Fig. 3*A*). Thus, high neuronal density in the telencephalon appears characteristic of all birds. This means that neuronal densities in the primate pallium are matched by those of chicken and emu, but surpassed by those of songbirds and parrots.

Discussion

Assuming that brains of parrots and songbirds have diverged from the presumptive ancestral avian pattern found in all representatives of basal bird lineages examined and characterized by a mammal-like numerical preponderance of cerebellar neurons, we suggest that birds generally have higher neuronal densities than mammals, and further that parrots and songbirds have acquired an expanded telencephalon with increased neuronal densities. Two proximate, synergistic mechanisms likely contributed to this evolutionary process. First, just like the expansion of neocortex in primates (52), the expansion of the telencephalon in parrots and songbirds is associated with delayed and protracted neurogenesis, an expanded subventricular zone, and delayed neuronal maturation (53–55). It has been suggested that extensive posthatching neurogenesis and brain maturation promote learning from conspecifics and may have facilitated the emergence of specialized circuits that mediate vocal learning and possibly also other flexible and innovative behaviors (56). Second, analyses of brain gene expression profiles strongly suggest that songbirds and parrots independently evolved vocal learning pathways by duplication of preexisting, surrounding motor circuits (57, 58). Intriguingly, parrot pallial song nuclei underwent a further duplication event to evolve a unique additional circuit, the so-called shell song system, which seems to be particularly well developed in large-brained parrots (45). What ultimate mechanisms drive the evolution of the enlarged, neuron-rich telencephalon, which sets parrots and songbirds apart from the more basal birds we examined, remains poorly understood. We suggest that this expansion has been due to simultaneous selective pressures on cognitive enhancement and an evolutionary constraint on brain size, which may stem from the constraints on body size imposed by active flight. Altriciality and the extended parental care that has developed in avian ancestors simultaneously relaxed constraints on the duration of ontogenesis, a precondition for telencephalic expansion by the mechanisms described above (56). Moreover, a short neck relative to many other bird lineages may have reduced biophysical constraints on head size (cf. ref. 59).

Our finding of greater than primate-like numbers of neurons in the pallium of parrots and songbirds suggests that the large absolute numbers of telencephalic neurons in these two clades provide a means of increasing computational capacity, supporting their advanced behavioral and cognitive complexity, despite their physically smaller brains. Moreover, a short interneuronal distance, the corollary of the extremely high packing densities of their telencephalic neurons, likely results in a high speed of information processing, which may further enhance cognitive abilities of these birds. Thus, the nuclear architecture of the avian brain appears to exhibit more efficient packing of neurons and their interconnections than the layered architecture of the mammalian neocortex.

Further comparative studies on additional species are required to determine whether the high neuronal densities and preferential allocation of neurons to the telencephalon represent unique features of songbirds, parrots, and perhaps some other clades like owls, or have evolved multiple times independently in large-brained birds. More detailed quantitative studies should assess the distribution of neurons among various telencephalic regions involved in specific circuits subserving specific functions. The results, combined with behavioral studies, will enable us to determine the causal relationships between neuronal numbers and densities and perceptual, cognitive, and executive/motor abilities, and greatly advance our understanding of potential mechanisms linking neuronal density with information-processing capacity.

Methods

Experimental procedures were all approved by the Institutional Animal Care and Use Committee at Charles University in Prague. Altogether, 73 birds belonging to 28 species were used in this study (Table S1). Animals were killed by an overdose of halothane and perfused with 4% (wt/wt) paraformaldehyde. Brains were removed, postfixed for an additional 7–21 d, and dissected into the cerebral hemispheres, cerebellum, diencephalon, tectum, and brainstem. In one individual per species, one hemisphere was dissected into the pallium and the subpallium. In these brain components, the total numbers of cells, neurons, and nonneuronal cells were estimated following the procedure of isotropic fractionation described earlier (40). The reduced major axis regressions to power functions were calculated to describe how structure mass, numbers of cells, and densities are interrelated across species. Analysis of covariance was used to compare scaling among groups (taxonomic orders or regions). To compare relative brain size between corvid and noncorvid songbirds, we computed *t* test on the residuals of a log–log regression of brain mass against body mass (residual brain mass, hereafter). For the comparison with cellular scaling rules reported previously for mammals, the reduced major axis regressions were calculated from quantitative data published for primates (33, 37, 38), rodents excluding the naked mole-rat (32, 39), and artiodactyls (36). In addition, the published quantitative data for Eulipotyphla (34) and Afrotheria (35) were used for comparison in Fig. S5. Further details are provided in *Supporting Information*.

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