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Numbers of neurons as biological correlates of cognitive capability

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What impact does variation in brain size have on the behavioral or cognitive capabilities of different species? Answering this seemingly simple question has been hampered by difficulties in defining and measuring the relevant variables in the brain, on the one hand, and in quantifying behavior in a way that can be compared across species, on the other. A new method of counting cells has made it easy to obtain direct estimates of the numbers of neurons that compose different brain structures. Crossing these numbers with the first large-scale quantitative studies of cognitive capabilities across species suggests that absolute numbers of neurons in the mammalian cerebral cortex, or in the bird pallium, are good correlates of cognitive diversity: the more the neurons, regardless of brain or body size, the better a species performs at a same task.

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Introduction

If the brain is the organ that directly organizes behavior, how does the enormous diversity in brain size, spanning a range of over one billion-fold across vertebrates and invertebrates, impact behavioral complexity and flexibility? The difficulty in answering this apparently simple question underscores how non-trivial it has been to quantify the two variables involved: behavior (should we measure repertoire size? Flexibility? Complexity? Speed of learning? Memory capacity? Self-control? And how should they be measured?) and brain diversity (is the relevant variable simply size? Should it be two-dimensional size, that is, surface area, or three-dimensional size, that is, volume? Number of neurons? Synapses? Glial cells? Fibers?).

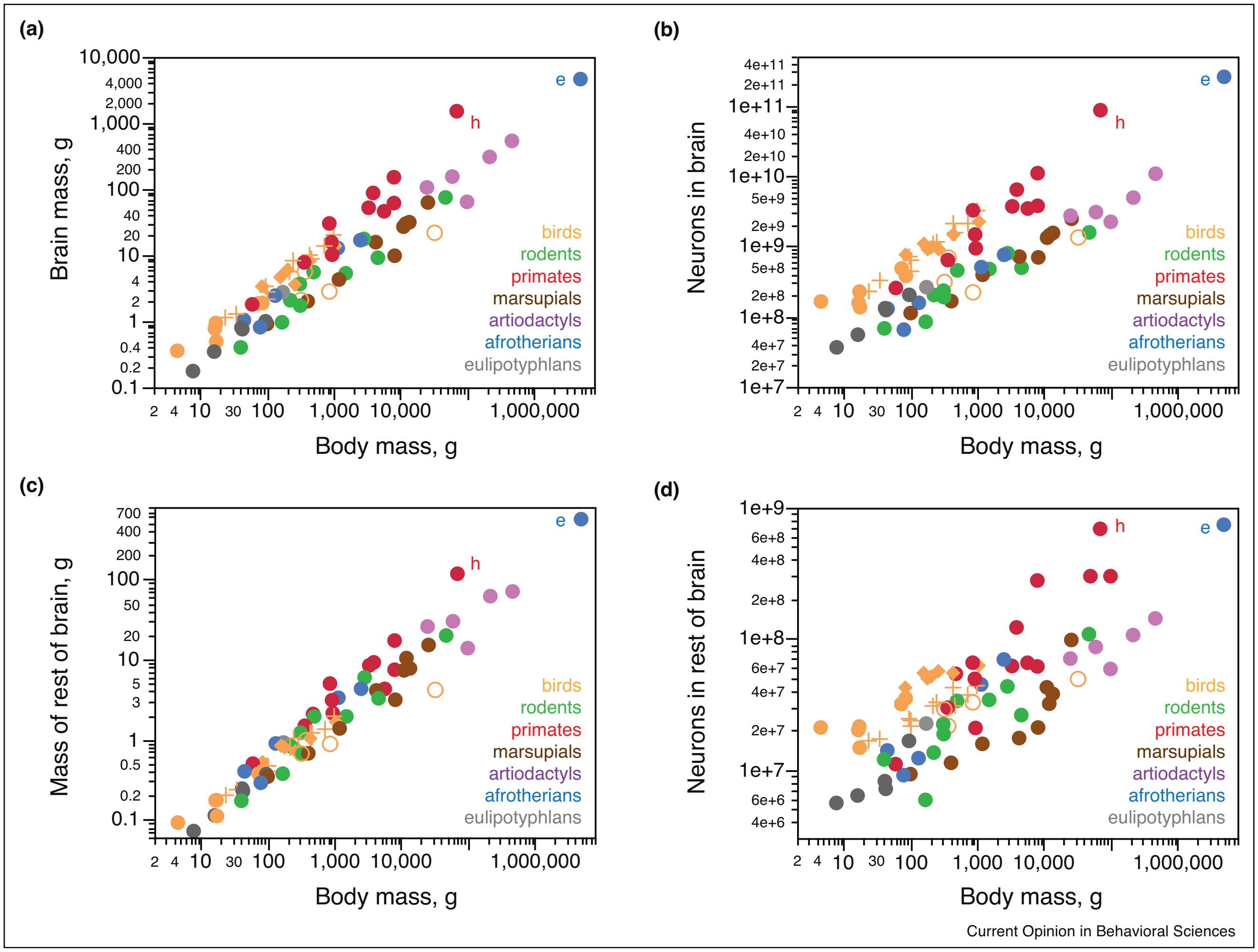
Brain tissue is made of neurons, glial cells and vasculature, and neurons are the functional units that integrate synaptic activity and pass it on. Across species spanning orders of magnitude differences in brain size, and given that brain organization is remarkably conserved within clades, the ultimate causes for diversity in behavioral capability (however it is measured) should thus lie on the numbers of neurons in well-defined circuits in the brain: the more the neurons that compose a circuit, the more the possibilities that the circuit in principle admits, just like duplicating an entire genome opens new venues for complexity in life. However, until recently, the numbers of cells that compose different brains were not available for analysis. The best proxies were morphometric variables such as brain or structure mass, volume, or surface area—besides whole body mass.

One problem with using brain mass as a proxy for whatever underlying brain features do correlate with behavioral capabilities is that brain mass (and the mass of its components) is very obviously correlated with body mass across species (Figure 1a). The problem is that if a larger body requires a larger brain to operate it, then increases in brain mass may not necessarily contribute to behavioral complexity beyond simple body control.

The usual solution to this problem has been to mathematically factor body mass out of the equation by assuming that there is a predictable component of brain mass, required to operate the body depending on the size of the latter, that can be estimated from body mass, then discounting it from total brain mass, which should 'neutralize' effects of body size. This is done by calculating quotients between actual values and those predicted allometrically from body mass (the basis of the encephalization quotient proposed by Jerison [1]), or by the related expedient of calculating the residuals for correlations between the variable of interest and body mass, in the hope of looking specifically at "what was left" after accounting for body mass.

The whole rationale behind the encephalization quotient and later analyses of residuals against body mass is that Jerison not only explicitly expected larger bodies to require more neurons to operate them, but also, predicting that the number of neurons in the brain is related to brain mass in a universal manner across species, proposed

Figure 1



Different scaling of brain mass, rest of brain mass, number of neurons in the brain and in the rest of brain with varying body mass.
Each point represents one species belonging to the different clades according to the colors in the legend. Among birds, Passeriformes are represented by orange filled circles and lozenges; psittaciformes by orange crosses; and barn owl, emu, pigeon and jungle fowl by unfilled orange circles. **(a)** Scaling of brain mass with body mass. Exponents, p-values and r^2 values for the different clades: afrotherians, 0.740 ± 0.033, $p < 0.0001$, 0.992; artiodactyls (minus pig), 0.548 ± 0.038, $p = 0.0048$, 0.990; eulipotyphlans, 0.727 ± 0.094, $p = 0.0045$, 0.952; marsupials, 0.742 ± 0.061, $p < 0.0001$, 0.955; primates, 0.903 ± 0.082, $p < 0.0001$, 0.931; rodents, 0.712 ± 0.071, $p < 0.0001$, 0.927; Passeriformes, 0.714 ± 0.051, $p < 0.0001$, 0.946; Psittaciformes, 0.785 ± 0.048, $p < 0.0001$, 0.968; all data points together, 0.674 ± 0.030, $p < 0.0001$, 0.876. **(b)** Scaling of the number of brain neurons with body mass. Exponents, p-values and r^2 values for the different clades: afrotherians, 0.695 ± 0.048, $p = 0.0001$, 0.982; artiodactyls (minus pig), 0.448 ± 0.115, $p = 0.0598$, 0.884; eulipotyphlans, 0.717 ± 0.045, $p = 0.0005$, 0.988; marsupials, 0.554 ± 0.041, $p < 0.0001$, 0.964; primates, 0.777 ± 0.091, $p < 0.0001$, 0.889; rodents, 0.452 ± 0.061, $p < 0.0001$, 0.872; Passeriformes, 0.570 ± 0.055, $p < 0.0001$, 0.908; Psittaciformes, 0.687 ± 0.040, $p < 0.0001$, 0.970; all data points, together, 0.456 ± 0.039, $p < 0.0001$, 0.651. **(c)** Scaling of the mass of the rest of brain (brainstem, diencephalon and striatum) with body mass. Exponents, p-values and r^2 values for the different clades: afrotherians, 0.640 ± 0.034, $p < 0.0001$, 0.989; artiodactyls (minus pig), 0.378 ± 0.056, $p = 0.0215$, 0.958; eulipotyphlans, 0.673 ± 0.034, $p = 0.0003$, 0.992; marsupials, 0.679 ± 0.055, $p < 0.0001$, 0.956; primates, 0.706 ± 0.076, $p < 0.0001$, 0.896; rodents, 0.656 ± 0.064, $p < 0.0001$, 0.923; Passeriformes, 0.582 ± 0.037, $p < 0.0001$, 0.958; Psittaciformes, 0.618 ± 0.029, $p < 0.0001$, 0.981; all data points, together, 0.629 ± 0.018, $p < 0.0001$, 0.940. **(d)** Scaling of the number of neurons in the rest of brain with body mass. Exponents, p-values and r^2 values for the different clades: afrotherians, 0.375 ± 0.036, $p = 0.0005$, 0.965; artiodactyls (minus pig), 0.227 ± 0.027, $p = 0.0136$, 0.973; eulipotyphlans, 0.383 ± 0.125, $p = 0.0548$, 0.758; marsupials, 0.349 ± 0.070, $p = 0.0017$, 0.778; primates, 0.484 ± 0.066, $p < 0.0001$, 0.816; rodents, 0.338 ± 0.072, $p = 0.0015$, 0.735; Passeriformes, 0.288 ± 0.039, $p < 0.0001$, 0.831; Psittaciformes, 0.264 ± 0.026, $p < 0.0001$, 0.919; all data points, together, 0.275 ± 0.025, $p < 0.0001$, 0.605. h, human data point; e, African elephant data point.

that the amount of extra tissue measured by his encephalization quotient could be converted into a measure of 'extra neurons' contained in that tissue [1]. Jerison acknowledged that numbers of neurons and glial cells would have been "more meaningful biological parameters" than brain mass, but in their absence, he argued that brain size could be used instead.

We now have enough data from 75 species (47 mammals and 28 birds) that allow us to examine numbers of neurons directly and how they relate to body mass or cognitive capability. All data available on total numbers of neurons in the brain or its main structures have been generated so far by our own group and collaborators using the isotropic fractionator [2], a non-stereological method based on dissolving fixed, dissected brain tissue and counting free cell nuclei that gives results comparable to those obtained with stereology but in much less time [3–5]. Using this method, we have directly estimated numbers of neurons in the brains of rodents [6,7], primates [8–10], eulipotyphlans [11], afrotherians [12,13], artiodactyls [14], marsupials [15], as well as different orders of birds [16]. As reviewed recently [17••,18], the data indicate that not only brain structure mass can be a misleading proxy for number of brain neurons (because of clade-specific relationships between numbers of neurons and neuronal density, which is inversely proportional to average neuronal cell size [19]), but there is also no universal relationship across mammalian or bird species between body mass and the number of brain neurons directly involved with operating the body.

Numbers of neurons in the brainstem should reflect body-related needs

However body mass influences or regulates numbers of neurons that directly or indirectly innervate and control body targets and sources of information, the number of neurons situated in structures most directly in contact with the body should offer a more direct proxy for the amount of neural processing involved with the body. Ideally, one would analyze numbers of neurons in the spinal cord; however, dissecting this organ in its integrity is a difficult task, and therefore many more brains than spinal cords are available for analysis. The brainstem, in contrast, is more easily available, provided that care is taken to section the medulla consistently at the level of the foramen magnum.

In our dataset, numbers of neurons are analyzed separately in three major brain structures: the cerebral cortex (including the white matter), the cerebellum, and the rest of brain (the ensemble of brainstem, diencephalon and striatum, excluding the olfactory bulbs, which are not consistently included in dissections). Neurons in the brainstem are directly connected either to the body or to first-order neurons in the central nervous system, and sensory signals are relayed to nuclei in the diencephalon. Thus, if any brain structure gains neurons in direct proportion to the scaling of the body, such gain should be apparent in the rest of brain: if a larger body requires more neurons to operate it, the rest of brain should gain neurons uniformly across species as body mass increases.

Indeed, the scaling of the mass of the rest of brain with increasing body mass appears much more concerted across mammalian and bird species than the scaling of brain mass as a whole (Figure 1a and c). However, this apparently concerted scaling conceals a highly clade-specific scaling of the number of neurons in the rest of brain with increasing body mass (Figure 1d), even more so than the scaling of the number of neurons in the whole brain with increasing body mass (Figure 1b). Notably, not only allometric exponents for the number of neurons in the rest of brain against body mass are significantly different across clades, but the scaling functions are also displaced even when scaling exponents are similar. For instance, rodents and marsupials have similar exponents of 0.338 ± 0.072 and 0.349 ± 0.070, respectively, but there are usually about twice as many neurons in the rest of brain of a rodent than in a marsupial of similar body mass. Likewise, within birds, passerines and psittacines have similar scaling exponents of 0.288 ± 0.039 and 0.264 ± 0.026, respectively, but there are typically about twice as many neurons in the rest of brain of the former than in the latter for a similar body mass (Figure 1d).

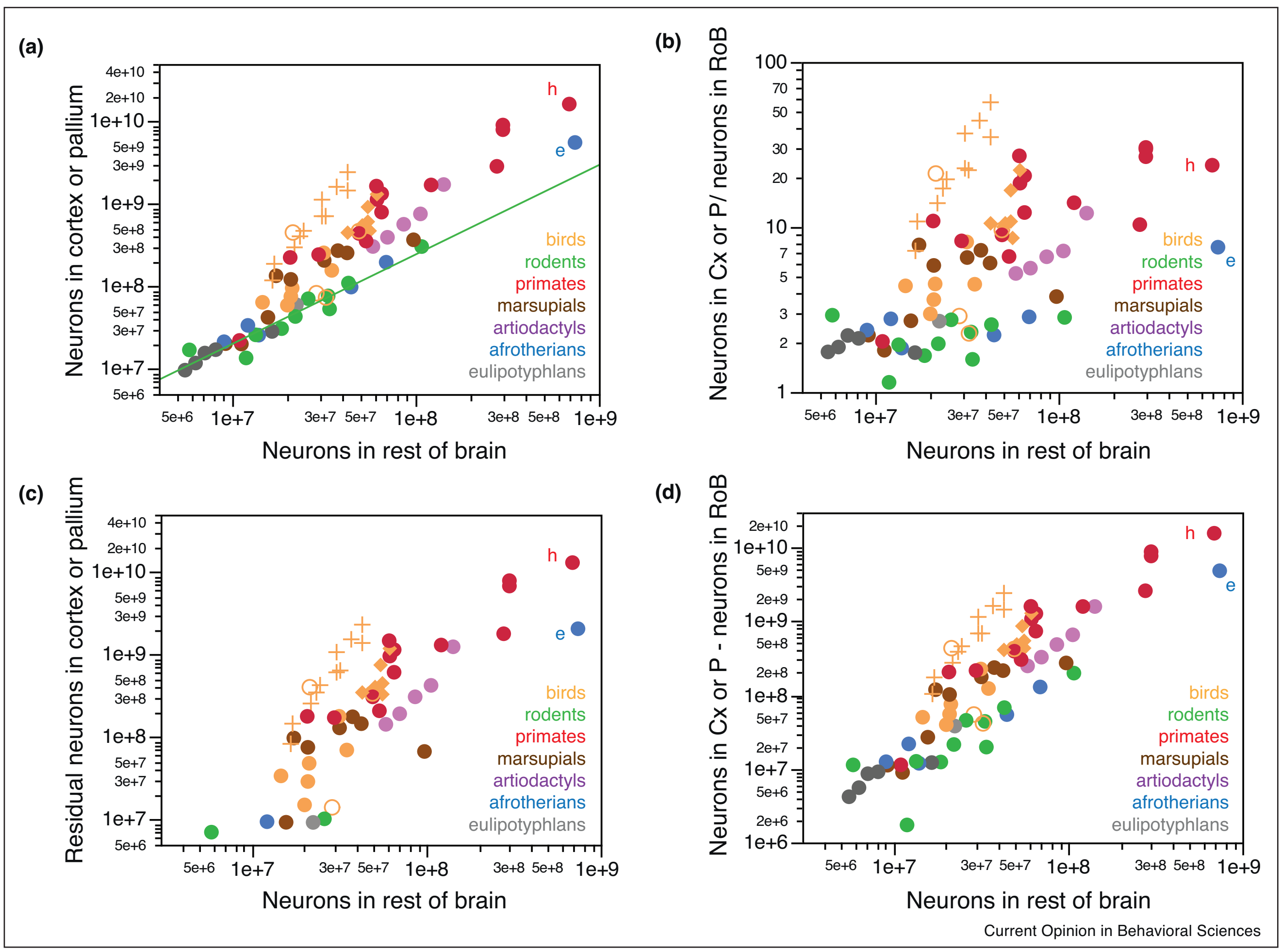
Although there is a general tendency towards more neurons in larger bodies, the number of neurons in the rest of brain does not vary across species as a *universal* function of body mass. While this may appear to argue against the very adequacy of using the number of neurons in the rest of brain as a proxy for the amount of body-related information processing depending on body size, I believe it calls instead for an important realization: that body mass is highly variable and not tightly correlated, much less universally correlated, with the make up of the brain that accompanies it. We have proposed that this is a consequence of body growth being much more flexible and variable than CNS development both across individuals and species [20]. Still, however variable body mass is, the amount of sensory, motor and visceral processing involved in operating the body must be limited by the number of neurons available in the brainstem (or rest of brain).

Variable scaling of numbers of neurons in the cerebral cortex and rest of brain

Although the 'rest of brain' in our dataset includes the diencephalon and striatum, it provides the best opportunity so far for examining how numbers of neurons in the main structure implicated in cognition, the cerebral cortex, increase in relation to the number of neurons involved in operating the body. Although organized in nuclei and not layers, the bird pallium shares a similar functional organization as the mammalian cerebral cortex [21•], fulfilling equivalent complex cognitive functions, thus providing a rationale for direct comparisons of numbers of neurons across the bird pallium and the mammalian cerebral cortex.

Comparing how absolute numbers of neurons in the cerebral cortex or pallium scale with numbers of neurons in the rest of brain (Figure 2a) informs on how neuron-based information processing capacity increases in one structure against the other. This analysis reveals that the two structures gain neurons proportionately in rodents, afrotherians and eulipotyphlans (Figure 2a, green line), which we have proposed to have been the ancestral proportion in which neurons were added to these two structures, from which other clades then departed [17••]. In primates, the cerebral cortex gains neurons with the number of neurons in the rest of brain raised to the power of 1.4, such that for a 10-fold increase in the number of neurons in the rest of brain, there is a 25-fold gain in number of cortical neurons (Figure 2a, red). In artiodactyls and passerine birds, the cerebral cortex or pallium

Figure 2



Scaling of numbers of neurons in the cerebral cortex or pallium against numbers of neurons in the rest of brain.
Each point represents one species belonging to the different clades according to the colors in the legend. Among birds, Passeriformes are represented by orange filled circles and lozenges; psittaciformes by orange crosses; and barn owl, emu, pigeon and jungle fowl by unfilled orange circles. **(a)** Scaling of absolute number of neurons in the cerebral cortex with absolute number of neurons in the rest of brain. Exponents, p-values and r^2 values for the different clades: afrotherians, 1.264 $\pm$ 0.073, $p < 0.0001$, 0.987; artiodactyls, 1.904 $\pm$ 0.172, $p = 0.0016$, 0.976; eulipotyphlans, 0.932 $\pm$ 0.142, $p = 0.0072$, 0.935; marsupials, 1.374 $\pm$ 0.245, $p = 0.0008$, 0.818; primates, 1.457 $\pm$ 0.120, $p < 0.0001$, 0.919; rodents, 1.103 $\pm$ 0.130, $p < 0.0001$, 0.900; Passeriformes, 2.089 $\pm$ 0.188, $p < 0.0001$, 0.918; Psittaciformes, 2.768 $\pm$ 0.212, $p < 0.0001$, 0.950; ensemble of afrotherians (minus the African elephant), eulipotyphlans and rodents, 1.089 $\pm$ 0.064, $p < 0.0001$, 0.938 (plotted); all data points together, 1.526 $\pm$ 0.093, $p < 0.0001$, 0.776. **(b)** Scaling of the ratio between numbers of neurons in the cerebral cortex of mammals (or pallium of birds) with the number of neurons in the rest of brain. **(c)** Scaling of the residual number of neurons in the cerebral cortex of pallium after regressing onto the number of neurons in the rest of brain, as in (a), with the absolute number of neurons in the rest of brain. **(d)** Scaling of the difference between number of neurons in the cerebral cortex or pallium and rest of brain with the absolute number of neurons in the rest of brain. h, human data point; e, African elephant data point.

gains neurons with approximately the square of the number of neurons in the rest of brain, such that for a 10-fold increase in the number of neurons in the rest of brain, there is a 100-fold increase in the number of neurons in the cerebral cortex or pallium (Figure 2A, pink and filled orange symbols). The gain in numbers of pallial neurons is even steeper in psittacine birds, with the number of neurons in the rest of brain raised to an exponent of 2.8 (Figure 2A, orange crosses). Importantly, the absolute number of neurons in the cerebral cortex is largest in humans, even in comparison to the African elephant, which we have proposed to underlie the cognitive superiority of the human species compared to others [13]. Corvids, the largest passerines, have similar numbers of pallial neurons as parrots and macaques [16]—although numbers of body-related neurons in the brainstem are much smaller in parrots (Figure 2a).

Another way to capture the differential addition of neurons to the cerebral cortex or pallium relative to the rest of brain is to plot the ratio between these numbers. Assuming that neurons in the cerebral cortex or pallium add complexity and flexibility to the processing of information that they receive from the rest of brain, this ratio serves as a proxy for the relative neuronal capability for complex information processing. Figure 2b shows that rodents, eulipotyphlans and small afrotherians have a fairly constant ratio of 2 neurons in the cerebral cortex per neuron in the rest of brain. The ratio increases with increasing numbers of neurons to the rest of brain in artiodactyls, primates and in birds, with larger ratios in primates than in artiodactyls with similar numbers of neurons in the rest of brain; similar numbers in primates and passerine birds; and very rapidly increasing ratios in psittacine birds (Figure 2b).

Relative metrics such as the ratio between numbers of neurons across structures have the problem of masking absolute values, however, which are probably much more relevant for the tasks involved. For instance, with a much smaller brain and fewer neurons in the pallium, parrots nevertheless have higher ratios of neurons between the pallium and rest of brain than macaques and even humans (Figure 2b). An alternative is calculating the residual number of neurons in the cerebral cortex (or pallium) after discounting the putative ancestral correlation that applies to some clades (Figure 2c)—or, even more simply, the arithmetic difference in numbers of neurons between the two structures (Figure 2d). Both calculations yield results that are very similar to the absolute number of neurons in the cerebral cortex or pallium (Figure 2a), given how small the number of neurons in the rest of brain in comparison. Thus, while the number of neurons in the rest of brain offers an interesting proxy for body-related neuronal processing, these neurons are so few compared to the cerebral cortex or pallium that the absolute number of neurons in the latter, regardless of the number of body-related neurons in the rest of brain, might be a simpler, more practical proxy for neuronal capability for complex information processing across species.

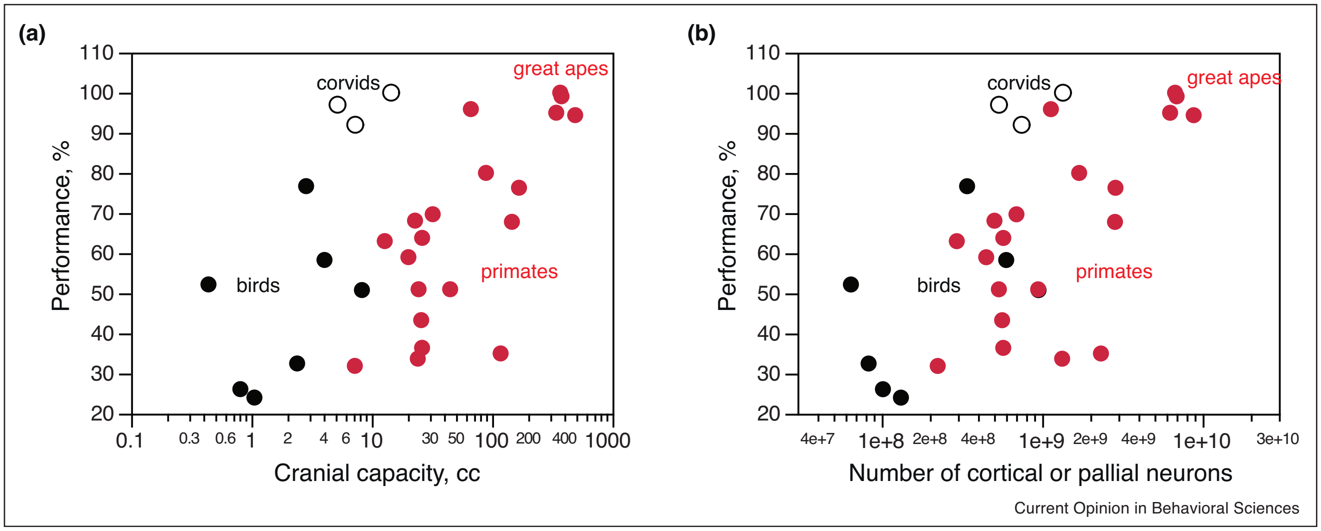
Comparing absolute numbers of neurons in the cerebral cortex or pallium across species reveals the largest numbers in humans (16 billion neurons), followed by gorilla and orangutan (9 billion), chimpanzee (6–7 billion), African elephant (5.6 billion), parrots, corvids, macaques and the giraffe (1–2 billion). In addition, psittacines have more neurons in the pallium (or cerebral cortex) than any other animal, bird or mammal, of similar brain size, including primates. The question that begs an answer then becomes: does this ranking of absolute number of cortical or pallial neurons match a ranking of cognitive capabilities across these species?

The need for comparable, quantitative behavioral data

The lack of systematic, comparative studies of cognitive capability across species has recently begun to be addressed. Comparative cognition is a difficult issue to tackle because of obvious hurdles to overcome, including making sure that tasks accommodate species-specific body form (paws, toes, claws, beak?), motivation, social anxiety, and non-trivial reasons why an animal does not perform (uncontrolled factors such as context, previous exposure, willingness to use different materials). Despite the difficulties and shortcomings still to be resolved, two large studies using complementary approaches were published in the last ten years, one only involving non-human primate species [22•] and the other, mostly primates [23••]. Both concluded that cognitive capability, measured either as a 'global cognition' index [22•] or using two self-control tasks [23••], did not scale with encephalization quotient, but did scale significantly with increasing absolute brain size.

A more recent study using a similar self-control task to [23••] found that corvids perform as well as great apes [24••], even though corvid brains are nearly 100 times smaller than great ape brains (Figure 3a). Combining the data in [23••] and [24••], we find that across birds and primates, there is hardly any overlap in the distribution of performance and brain size (in this case, as estimated by cranial capacity; Figure 3a). Interestingly, plotting performance in this self-control task as a function of the total number of neurons in the cerebral cortex or pallium of these species brings birds and primates much closer together, and now corvids overlap with the rhesus macaque in both variables (Figure 3b). Considering the likelihood of a ceiling effect for the task, it is tempting to speculate that regardless of their small body and brain size or number of neurons in the rest of brain, corvids have attained the number of pallial neurons required to perform the complex information processing required to solve the task.

Figure 3



Relationship between performance in a cognitive task and brain size or number of cortical neurons.
Each point represents one species of birds (black) or primates (red). Data on behavioral performance from [23••]; data on numbers of cerebral cortical neurons from [16,18]. Corvids studied in [23••] and indicated by the unfilled circles. **(a)** % correct performance in the cylinder task as a function of cranial capacity (in cc). **(b)** % correct performance as a function of the number of neurons in the pallium or cerebral cortex of each species.

Total numbers of neurons in the cerebral cortex or pallium, however, still include neurons that are involved in purely sensory or motor functions, whereas complex cognition, while obviously relying on sensorimotor cortical processing, engages associative areas. Future studies should address how numbers of neurons specifically in associative regions of cerebral cortex or pallium compare across species. We have recently shown that across human and non-human primates alike, the prefrontal region holds a similar 8% of all neurons in the cerebral cortex—which translates into a much larger absolute number of neurons in humans than in any other primate [25••]. Our preliminary data on birds suggest that the associative regions of the pallium that correspond in functional connectivity to the mammalian prefrontal cortex [21•], including the nidopallium caudolaterale, concentrate at least 10% of all pallial neurons (Felix Ströckens, Kleber Neves, SHH and Onur Güntürkün, unpublished observations). The corvid pallium might thus match or even exceed the cerebral cortex of macaques in numbers of neurons dedicated to associative functions.

Conclusions

The history of the search for neural correlates of variation in cognitive capabilities across species has involved a long tradition of using brain and body mass and making assumptions about how they reflect underlying numbers of neurons. Now that numbers of neurons can be estimated rapidly and reliably, one side of the equation has been taken care of; what the field badly needs are more systematic quantitative studies of behavior and cognition that can be crossed to those data in search of an answer to the simple, but elusive question: what does it mean to have a bigger brain?

Conflict of interest statement

I hereby declare having no conflicts of interest regarding the manuscript.

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- • of special interest
- •• of outstanding interest

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A large consortium of authors gathered efforts to quantitatively compare the cognitive performance of 567 individuals of 36 species of birds and mammals using two problem-solving tasks requiring self-control. Despite the inevitable shortcomings involved with presenting so many species with the same two tasks, this is a tour de force that will hopefully pave the way to much needed similar quantitative, comparative studies of cognitive capabilities.

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Complementing the study by MacLean et al. [22], the authors examine self-control in three species of corvids and show that, despite their small brain size, their capacity is similar to that of great apes in solving the same task.

25. •• Gabi M, Neves K, Masseron C, Ventura-Antunes L, Ribeiro P, Torres L, Kaas JH, Herculano-Houzel S: **No expansion in numbers of prefrontal neurons in primate and human evolution**. *Proc Natl Acad Sci U S A* 2016, **113**:9617-9622.
Up to this point, all studies that provided evidence of preferential expansion of the prefrontal cortex in human evolution had been based solely on brain volumes. This study address directly how the distribution of numbers of neurons along the cerebral cortex compares across human and non-human primates, and found that the prefrontal region holds the same 8% of all cortical neurons in all species, indicating that the human prefrontal cortex is expanded in absolute, but not relative, numbers of neurons.