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Encephalization, Neuronal Excess, and Neuronal Index in Rodents

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ABSTRACT

Encephalization, or brain size larger than expected from body size, has long been considered to correlate with improved cognitive abilities across species and even intelligence. However, it is still unknown what characteristics of relatively large brains underlie their improved functions. Here, it is shown that more encephalized rodent species have the number of neurons expected for their brain size, but a larger number of neurons than expected for their body size. The number of neurons in excess relative to body size might be available for improved associative functions and, thus, be responsible for the cognitive advantage observed in more encephalized animals. It is further proposed that, if such neuronal excess does provide for improved cognitive abilities, then the *total* number of excess neurons in each species—here dubbed the neuronal index—should be a better indicator of cognitive abilities than the encephalization quotient (EQ). Because the neuronal index is a function of both the number of neurons expected from the size of the body and the absolute number of neurons in the brain, differences in this parameter across species that share similar EQs might explain why these often have different cognitive capabilities, particularly when comparing across mammalian orders. Anat Rec, 290:1280–1287, 2007. © 2007 Wiley-Liss, Inc.

Key words: encephalization; number of neurons; number of glia; brain size; brain allometry; evolution; rodents; comparative neuroanatomy

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How brain properties such as absolute and relative size and number of neurons relate to cognitive abilities has been a long-standing question in neuroscience. One widely used parameter is the encephalization quotient (EQ), defined by Jerison (1973, 1977). EQ was first proposed as a useful parameter based on the observation that some animals, humans foremost, seem to have larger brains than expected from their body size.

The meaning of EQ relies on the observation that, despite the large range of brain sizes found in nature, varying over 100,000 times among mammals (Haug, 1987), brain mass increases together with body mass across species in a manner that can be described mathematically by a power law (von Bonin, 1937). This allows the expected brain mass of any species to be calculated from its body mass (Jerison, 1973; Martin, 1981; Hofman, 1982; Foley and Lee, 1991).

Actual brain mass, however, differs significantly from the expected in some species in a way that has been suggested to be functionally significant. The deviation from the expected brain mass is often described by the EQ, defined by Jerison (1973, 1977) as the ratio between observed and expected brain mass. Larger EQs thus describe species whose average brain mass is much larger than expected from their body mass.

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Of interest, much evidence suggests that larger EQs or relative brain size endow species with improved cognitive abilities (Lefebvre et al., 2004); with behavioral flexibility, such as the ability to respond successfully to novel environments (Sol et al., 2005) or to alternate between feeding strategies (Ratcliffe et al., 2006); and even correlate with intelligence (Jerison, 1985). These findings seem to agree with the fact that humans, dolphins, and chimpanzees have the largest known EQs (Marino, 1998).

Despite the number of studies relating encephalization to behavioral capabilities and the general notion that larger cortices endow species with better cognitive power (Hofman, 1982), it is still not known what aspects of larger than expected brains would give rise to the associated cognitive benefits. Our recent account of the cellular scaling rules that determine the neuronal composition of rodent brains (Herculano-Houzel et al., 2006) raised the opportunity to use data on total numbers of neurons in the brain of different rodent species to examine how encephalization might relate to deviations from the expected cellular composition of the brain. For this end, four new parameters were defined: somatic neuronal quotient (SNQ), which describes how the total number of neurons in the brain or a brain structure deviates from the expected for a rodent of a given body size; somatic glial quotient (SGQ), which describes how the total number of non-neuronal cells deviates from the expected for a rodent of a given body size; encephalic neuronal quotient (ENQ), which describes how the total number of neurons in the brain or a brain structure deviates from the expected for a rodent of a given brain or brain structure size; and encephalic glial quotient (EGQ), which describes how the total number of non-neuronal cells deviates from the expected for a rodent of a given brain or brain structure size. The analysis of each of these parameters against EQ indicates directly how encephalization in rodents might relate to deviations from the expected cellular composition of the brain.

MATERIAL AND METHODS

All analyses are based on data published recently on body mass, brain mass, and total numbers of neuronal and non-neuronal cells in the cortex, cerebellum, and remaining brain areas of six rodent species: mouse, hamster, rat, guinea pig, agouti, and capybara (Herculano-Houzel et al., 2006; see supplemental information therein).

The relationship between each variable and body size was determined by regression to power functions using Statview 5.0 software (SAS, EUA). In that data set, the expected brain mass (EM_{brain}) for rodents is found to scale with body mass (M_{body}) according to the equation $EM_{brain} = 0.026 \times {M_{body}}^{0.773}$. This equation yields expected brain masses that are overall closer to the observed values than those obtained by applying Jerison's equation $EM_{brain} = 0.12 \times {M_{body}}^{0.667}$, derived from data compiled across several mammalian orders, primates included (Jerison, 1973). Using the equation from our own data set, EQ was calculated for each rodent specimen separately as the ratio between its observed and expected brain masses. The EQ for each species

TABLE 1. Allometric equations[a]

	Cerebral cortex	Cerebellum	Remaining structures
Structure mass × body mass	$EM_{cx} = 0.009 \times {M_{body}}^{0.826}$	$EM_{cb} = 0.005 \times {M_{body}}^{0.725}$	$EM_{re} = 0.015 \times {M_{body}}^{0.712}$
Neurons in structure × body mass (for SNQ)	$EN_{cx} = 2.39 \times 10^6 \times {M_{body}}^{0.460}$	$EN_{cb} = 6.80 \times 10^6 \times {M_{body}}^{0.517}$	$EN_{re} = 3.74 \times 10^6 \times {M_{body}}^{0.345}$
Neurons in structure × Structure mass (for ENQ)	$EN_{cx} = 33.47 \times 10^6 \times {M_{cx}}^{0.556}$	$EN_{cb} = 312.56 \times 10^6 \times {M_{cb}}^{0.715}$	$EN_{re} = 29.66 \times 10^6 \times {M_{re}}^{0.503}$
Non-neuronal cells in structure × body mass (for SGQ)	$EG_{cx} = 926.94 \times 10^3 \times {M_{body}}^{0.729}$	$EG_{cb} = 572.63 \times 10^3 \times {M_{body}}^{0.664}$	$EG_{re} = 2.40 \times 10^6 \times {M_{body}}^{0.560}$
Non-neuronal cells in structure × structure mass (for EGQ)	$EG_{cx} = 60.90 \times 10^6 \times {M_{cx}}^{0.885}$	$EG_{cb} = 76.25 \times 10^6 \times {M_{cb}}^{0.898}$	$EG_{re} = 69.64 \times 10^6 \times {M_{re}}^{0.823}$

[a] SNQ, somatic glial quotient; ENQ, encephalic neuronal quotient; SGQ, somatic glial quotient; EGQ, encephalic glial quotient; M_{body}, body mass; M_{cx}, mass of the cerebral cortex; M_{cb}, mass of the cerebellum; M_{re}, mass of the remainder of brain; EM_{cx}, expected mass of cerebral cortex; EM_{cb}, expected mass of cerebellum; EM_{re}, expected mass of remainder of brain; EN_{cx}, expected number of neurons in cerebral cortex; EN_{cb}, expected number of neurons in the cerebellum; EN_{re}, expected number of neurons in the remainder of brain; EG_{cx}, expected number of glial cells in the cerebral cortex; EG_{cb}, expected number of glial cells in the remainder of brain; EG_{re}, expected number of glial cells in the remainder of brain.

was then calculated as the average of all specimens examined.

Because the total number of neurons in the brain has been shown to vary allometrically with both body and brain mass (Herculano-Houzel et al., 2006), a similar method was used to calculate an SNQ for each specimen: the ratio between the observed number of neurons in the brain and the expected number of neurons in the brain (EN_{brain}) given the animal's body mass according to the equation $EN_{brain} = 13.28 \times 10^6 \times M_{body}^{0.461}$ (from Herculano-Houzel et al., 2006). The SNQ for each species was then calculated as the average of all specimens examined. Because the number of neurons in the rodent cerebral cortex, cerebellum, and remaining areas also scale allometrically with body mass, an SNQ was also calculated for each of these brain regions according to the equations in Table 1.

The same method was applied to calculate SGQ for the whole brain and each of its regions, as the ratio between the observed number of non-neuronal cells in the brain (or region thereof) and the expected number of non-neuronal cells in the brain (EG_{brain}), given the animal's body mass according to the equation $EG_{brain} = 3.70 \times 10^6 \times M_{body}^{0.643}$ and the equations given in Table 1.

As the total numbers of neuronal and non-neuronal cells are also related to the mass of each structure or total brain mass, an encephalic neuronal quotient (ENQ) as well as an encephalic glial quotient (EGQ) were then calculated for each species as the ratio between the observed and expected number of neurons or non-neuronal cells in the brain (according to the equations $EN_{brain} = 118.64 \times 10^6 \times M_{brain}^{0.613}$ and $EG_{brain} = 78.60 \times 10^6 \times M_{brain}^{0.856}$) and in each of its divisions, given the mass of these structures, according to the equations in Table 1.

The different quotients (SNQ, SGQ, ENQ, and EGQ) were then subjected to regression analysis for correlations with EQ across the rodent species. Correlations between residuals of the regressions of total number of neurons and non-neuronal cells in the brain and brain mass onto body mass were also computed.

RESULTS

Of the six rodent species analyzed, the most encephalized are the guinea pig and the agouti, with brains over 50% larger than expected from body size, and the least encephalized are the hamster and the capybara, whose brains are over 25% smaller than expected for their body size (Table 2). Variations in EQ across these species do not correlate significantly with parameters such as total numbers of neuronal or non-neuronal cells, fractional size of each brain structure, their absolute or fractional number of neurons, or neuronal density (all *P* values well above 0.05; data not shown).

Of interest, SNQ is found to vary in the same range as EQ, and the two species with the largest and smallest EQs also have the largest and smallest SNQs, respectively (Table 2). SNQ varies as a power function of EQ across the six species ($P = 0.0400$; Fig. 1a); a similar function relates the average SNQ and EQ across individuals of the six species ($P = 0.0011$; not shown). This finding suggests that larger than expected rodent brains

TABLE 2. Encephalization and somatic neuronal and cerebral neuronal quotients in rodent species[a]

Species	Body mass (g)	Brain mass (g)	EM_{brain} (g)	EQ	N (millions)	EN_{brain} (millions)	NI (millions)	SNQ	ENQ	G (millions)	EG_{brain} (millions)	SGQ	EGQ
Mouse (n = 4)	40.4 ± 11.6	0.416 ± 0.028	0.452 ± 0.098	0.949 ± 0.187	70.89 ± 10.41	72.58 ± 9.07	−1.68 ± 10.83	0.982 ± 0.153	1.021 ± 0.119	37.80 ± 6.66	39.63 ± 7.05	0.976 ± 0.246	1.014 ± 0.123
Hamster (n = 2)	168.1 ± 13.6	1.020 ± 0.147	1.365 ± 0.085	0.745 ± 0.061	89.97 ± 10.41	140.91 ± 5.26	−50.94 ± 4.29	0.638 ± 0.044	0.750 ± 0.013	76.15 ± 14.22	99.69 ± 5.19	0.761 ± 0.103	0.949 ± 0.061
Rat (n = 4)	315.1 ± 102.9	1.802 ± 0.313	2.205 ± 0.547	0.828 ± 0.080	200.13 ± 12.17	182.62 ± 26.83	13.51 ± 33.80	1.090 ± 0.179	1.191 ± 0.167	131.52 ± 6.11	148.11 ± 30.20	0.914 ± 0.177	1.031 ± 0.176
Guinea pig (n = 2)	311.0 ± 49.1	3.759 ± 0.499	2.195 ± 0.269	1.711 ± 0.018	239.62 ± 279	186.91 ± 13.66	52.72 ± 16.45	1.286 ± 0.109	0.901 ± 0.084	238.24 ± 13.36	147.92 ± 15.06	1.614 ± 0.074	0.980 ± 0.057
Agouti (n = 3)	2843.3 ± 195.5	18.365 ± 2.061	12.152 ± 0.647	1.519 ± 0.231	856.74	518.98 ± 16.51	355.01	1.708	1.178	1038.19	614.34 ± 27.23	1.772	1.050
Capybara (n = 2)	47500.0 ± 3535.5	76.036 ± 3.787	107.140 ± 6.167	0.710 ± 0.006	1601.12 ± 81.16	1900.71 ± 65.27	−299.59 ± 15.89	0.842 ± 0.014	0.949 ± 0.019	3265.32 ± 999.60	3756.03 ± 179.86	0.864 ± 0.225	1.014 ± 0.269

[a] EM_{brain}, expected brain mass, calculated from the allometric relationship between rodent body and brain size (9); EQ, encephalization quotient, calculated as the ratio between observed brain mass and EM_{brain}; N, total number of neurons found in the brain; EN_{brain}, total number of neurons expected from the allometric relationship between rodent body size and number of neurons in the brain; NI, neuronal index (N - EN_{brain}); SNQ, somatic neuronal quotient (the ratio between N and EN_{brain}); ENQ, encephalic neuronal quotient (the ratio between N and the total number of neurons in the brain expected from the allometric relationship between brain size and number of neurons); G, total number of non-neuronal cells found in the brain; EG_{brain}, total number of non-neuronal cells expected from the allometric relationship between rodent body size and number of non-neuronal cells in the brain; SGQ, somatic glial quotient (the ratio between G and EG_{brain}); EGQ, encephalic glial quotient (the ratio between G and the total number of non-neuronal cells in the brain expected from the allometric relationship between brain size and number of non-neuronal cells).

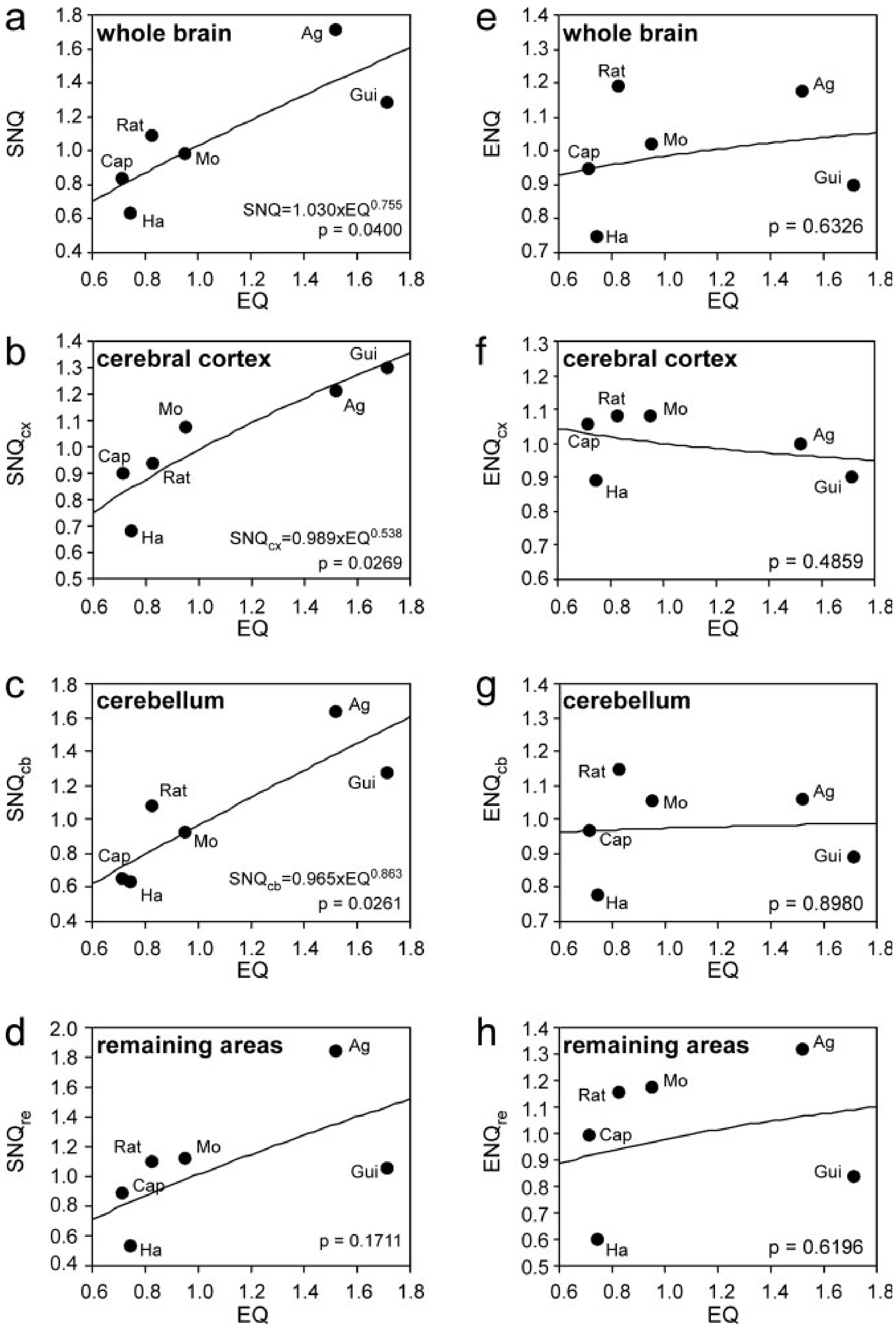

Fig. 1. Larger than expected brains have more neurons than expected from body size, but not from brain size. **a–h:** Graphs depict how encephalization quotients (EQ) correlate with deviations from the number of neurons expected from body size (somatic neuronal quotients or SNQ, a–d) and from brain size (encephalic neuronal quotients or ENQ, e–h) for whole brain (a,e), cerebral cortex (b,f), cerebellum (c,g), and remaining areas (d,h). Each point represents the average values for each of six rodent species. Ag, agouti; Cap, capybara; Gui, guinea pig; Ha, hamster; Mo, mouse; Rat, rat. Power functions are given whenever the *P* values (indicated in each graph) are <0.05.

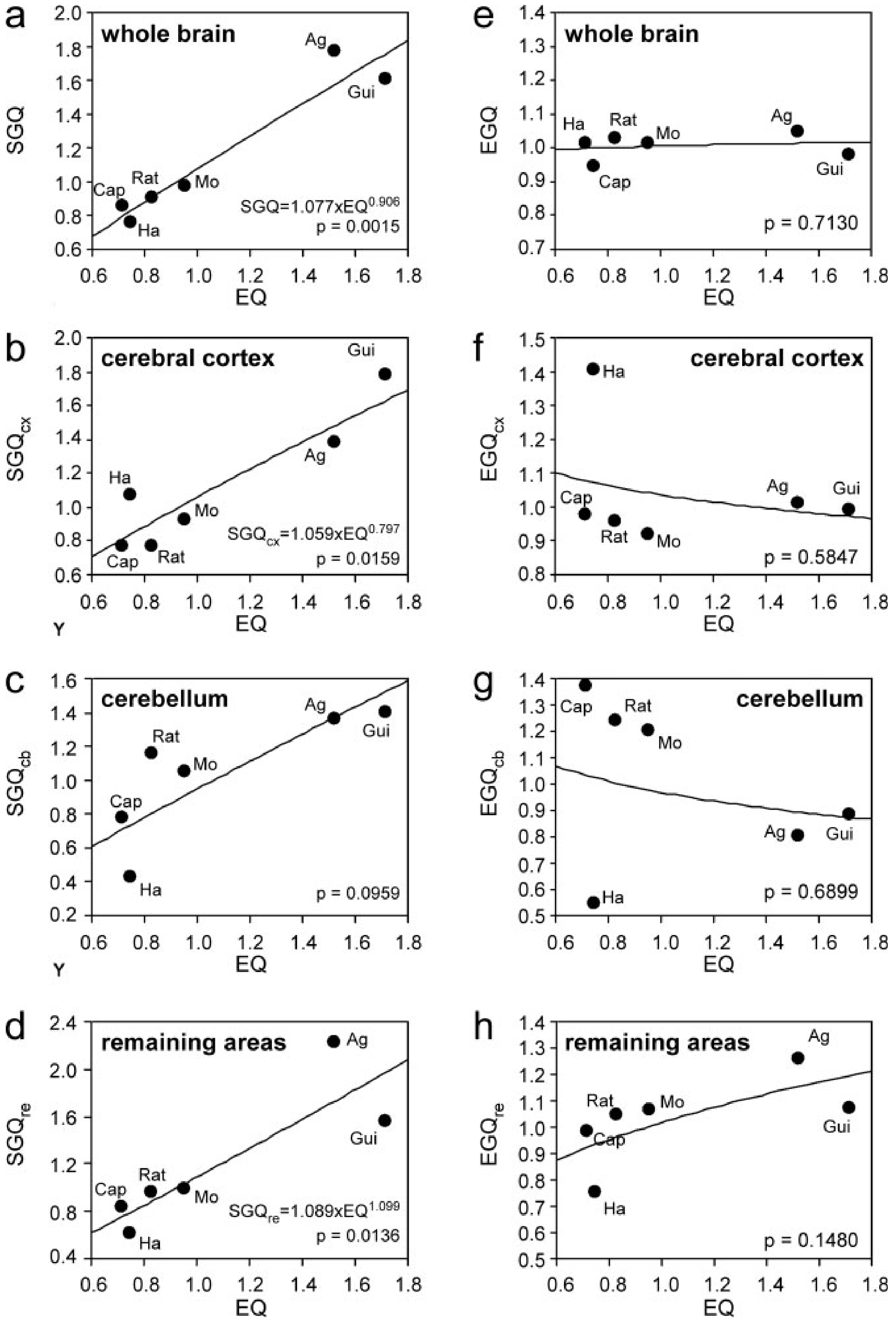

Fig. 2. Larger than expected brains have more non-neuronal cells than expected from body size, but not from brain size. **a–h:** Graphs depict how encephalization quotients (EQ) correlate with somatic glial quotients (SGQ, a–d) and encephalic glial quotients (EGQ, e–h) for whole brain (a,e), cerebral cortex (b,f), cerebellum (c,g), and remaining areas (d,h). Each point represents the average values for each of six rodent species. Ag, agouti; Cap, capybara; Gui, guinea pig; Ha, hamster; Mo, mouse; Rat, rat. Power functions are given whenever the *P* values (indicated in each graph) are <0.05.

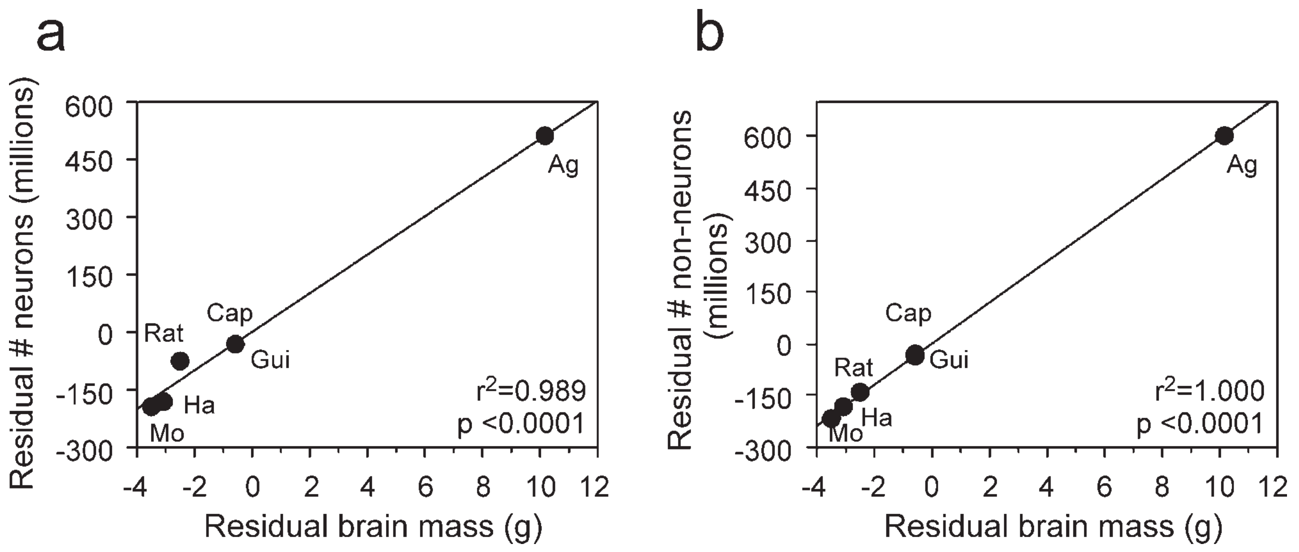

Fig. 3. Larger than expected brains have more neurons and non-neuronal cells than expected from body mass. **a,b:** Residuals of the allometric relation between number of neurons (a) or non-neuronal cells (b) in the brain and body mass (*y*-axis, in millions of cells) correlate linearly with residuals of the allometric relation between brain and body mass (*x*-axis, in grams).

are composed of more neurons than expected for their body size.

Regression to power functions shows that SNQ in the cerebral cortex (Fig. 1b) and cerebellum (Fig. 1c), but not in the remaining areas (Fig. 1d), covaries with EQ. This finding means that cerebral cortices and cerebella in larger than expected rodent brains, but not the remaining areas, are composed of more neurons than expected from body size.

In contrast to somatic quotients, ENQ varies much less than SNQ and does not correlate with EQ, neither for the whole brain nor for the subdivisions examined (Fig. 1e–h), suggesting that encephalization is not related to how the neuronal composition of the whole brain and its various structures departs from the expected given brain size.

Similar results were obtained overall for the comparison of glial quotients calculated in a similar manner to SNQ and regional CNQs (Fig. 2a–h), except that the correlation between cerebellar SGQ and EQ failed to reach significance (Fig. 2c), while the power function relating remaining areas SGQ and EG does (Fig. 2d). These findings suggest that, although encephalized species possess more neurons and glial cells than expected for their body size, the cellular composition of their brains does not differ significantly from the expected for their brain size.

Another means of evaluating how encephalization relates to an excessive number of neurons is through the comparison of the residuals of the regressions of brain size and number of neurons or non-neuronal cells against body mass. These residuals are found to be strongly correlated ($r^2 = 0.989$ and 1.000, respectively; Fig. 3), confirming the association between encephalization and a higher number of neurons and non-neuronal cells in the brain than expected for a given body size.

Like EQ, quotients between actual and expected number of neurons and non-neuronal cells do not take into consideration the absolute size of the animal or its brain. This would suggest that small and large animals with the same EQ or SNQ should have similar cognitive abilities, which may not be the case. An alternative to ranking species by EQ or SNQ would be to establish the total number of excess neurons in each species, hereafter referred to as the neuronal index (Table 1), which adjusts the quotient of excess neurons given the size of the body by taking into consideration the absolute number of neurons in the brain. The difference between ranking rodent species by EQ, SNQ, or neuronal index is shown in Figure 4, which demonstrates that the latter criterion singles out the agouti with a larger neuronal index than the guinea pig, despite the agouti's smaller EQ, and the capybara with a markedly low neuronal index, despite its moderately low EQ and SNQ compared with the hamster.

DISCUSSION

The direct relationship between encephalization quotients and somatic neuronal quotients in the absence of any relationship between encephalization quotients and encephalic neuronal quotients indicates that more encephalized species have a higher number of neurons in excess for a given body size, while having just as many neurons as expected for their brain size. Thus, although having a brain whose cellular composition complies with the cellular scaling rules for the order (Herculano-Houzel et al., 2006), more encephalized rodent species may have more neurons than would be necessary to deal with sensorimotor and vegetative information pertaining to a body of their size. This statement is in contrast to Jerison's (1973) notion that it is the volume, not the number of neurons, that determines the "information processing capacity" of brain tissue.

Still according to Jerison (1973), total brain weight (E) can be considered the sum of two independent components: E_v, determined by body size, and E_c, associated with improved adaptive capacities. It is interesting to

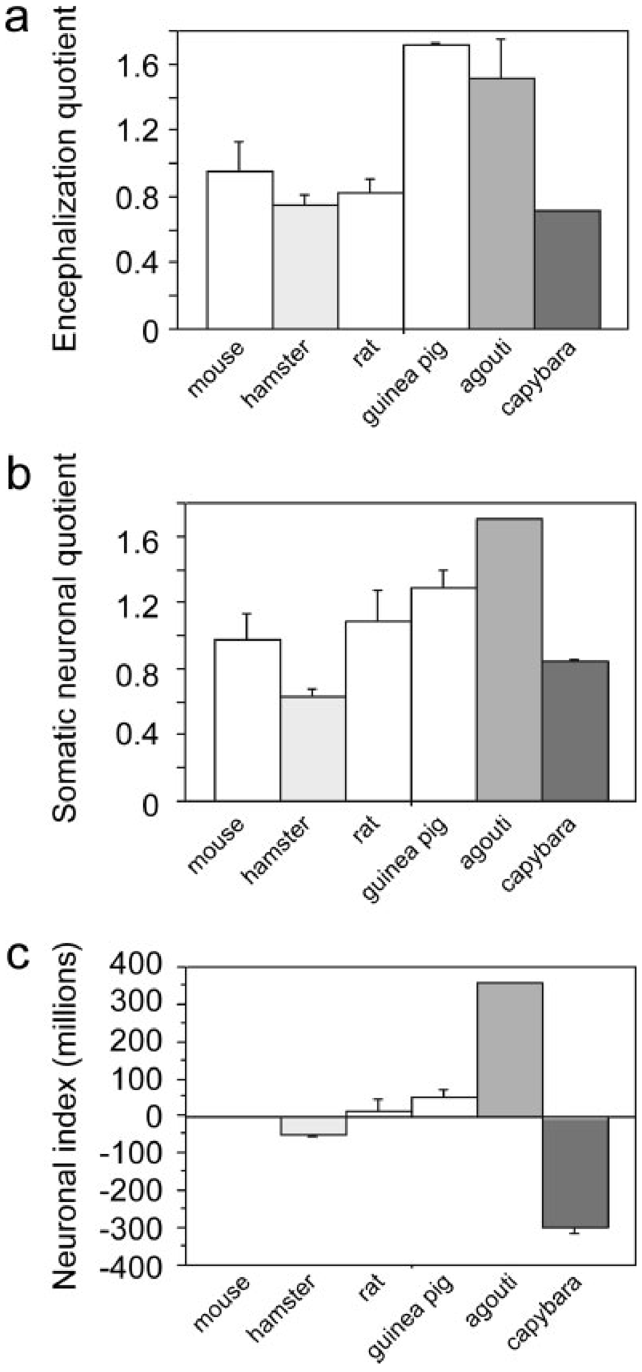

Fig. 4. Rodent species are ranked differently by encephalization quotient (EQ), somatic neuronal quotient (SNQ), and neuronal index (NI, or total number of excess neurons). **a:** Shown is the ratio between observed brain mass and that expected from body size (EQ) of six rodent species, ordered by brain mass. **b:** The ratio between observed number of brain neurons and that expected from body mass (SNQ) of the same species shown in the same order as in a. **c:** Number of brain neurons above or below that expected from body mass (NI) of the same species shown in a and b. Bars indicate average values ± standard deviation.

consider that variations in SNQ correlated with EQ might correspond to variations in the number of neurons that compose E_c. Thus, a higher number of supernumerary neurons available for associative, nonsomatic functions could account for the increased cognitive flexibility that has been observed in encephalized animals (Lefebvre et al., 2004). In this regard, it is fitting that the deviation in the number of neurons expected from body size (SNQ) for the noncortical, noncerebellar areas of the brain, which have mostly somatic functions, does not covary significantly with EQ. Thus, presumably by providing larger associative computational possibilities, larger numbers of neurons than expected from body size in the cerebral cortex and cerebellum, rather than absolute number of neurons or the absolute or relative size of these areas, would be expected to bring improved cognitive abilities across species.

Both EQ and SNQ, however, fail to take into consideration absolute size of brain structures, which has been shown to be related to some abilities, like deception in primates (Byrne and Corp, 2004). By definition, a large brain of large EQ would be expected to have much more excess brain mass than a small brain of similarly large EQ. Interestingly, however, Jerison expected that “when the larger-bodied species is encephalized to the same extent as the smaller one, it should have the same number of ‘extra neurons’ as the smaller species” (Jerison, 1985). This expectation was based on the smaller density of neurons in larger than smaller brains (Tower and Elliott, 1952; Tower, 1954; Jerison, 1963). In contrast, the rodent data analyzed here show that the agouti, which has a similar EQ to the guinea pig, does have a much larger number of “extra neurons”—the neuronal index—than the guinea pig, which has the smaller brain. This finding is the case despite the smaller neuronal density found in larger rodent brains (Herculano-Houzel et al., 2006).

If a higher than expected number of neurons in the brain, given the species body size, does provide for improved cognitive abilities, then the *total* number neurons in excess of the expected from body size in each species (the neuronal index) might be a better indicator of cognitive abilities than EQ. The neuronal index should also be a better predictor of cognitive abilities than absolute number of neurons (Roth and Dicke, 2005), which fails to take body size into consideration. Different neuronal indices would settle the question of whether small and large animals of the same mammalian order with similar EQs should have similar cognitive abilities. With a larger neuronal index, for example, the agouti would be expected to have better cognitive abilities than the guinea pig, despite the larger EQ of the latter, and the capybara would be expected to have markedly fewer abilities than the hamster, despite their comparably low EQs. Comparative studies on the cognitive abilities of rodent species and species of other mammalian orders should establish which is a more accurate predictor of cognitive abilities: EQ, absolute number of neurons or neuronal index.

The proposition of the neuronal index as a novel parameter to examine cognitive abilities opens new conceptual and experimental possibilities for investigation that might solve incongruencies such as the superior abilities of chimpanzees and gorillas compared with capuchin monkeys, despite the larger EQ of the latter (Jerison, 1973). In general, of two animals of the same mammalian order with similar EQs, the species with the larger brain, and therefore the larger neuronal index, would be expected to have superior cognitive abilities and a larger behavioral repertoire than the other. In line with this suggestion, it has recently been shown that, among nonhuman primates, absolute brain size measures are better predictors of cognitive ability than EQ (Deaner et al., 2007). It will be interesting to determine the neuronal index of these primate species once their total numbers of neurons in the brain become available.

A similar argument would apply to animals of *different* orders, such as primates and cetaceans. Although several cetaceans are found to have EQs larger than those of all nonhuman primates, their low neuronal densities in the cerebral cortex (Tower, 1954) compared with the higher densities found in primates might lead to a small number of excess neurons, if at all, relative to the expected from their body size. With larger EQs but possibly smaller neuronal indices than most primates, cetaceans might therefore be expected, after all, *not* to have the same cognitive abilities as primates of same EQ. Indeed, the abilities of the dolphin have recently been questioned (Manger, 2006).

By adjusting the proportion of excess neurons to the absolute number of neurons in the brain, the neuronal index would also explain how complex cognitive functions may be achieved in humans and great apes by isometric scaling of associative brain regions such as frontal cortex (Semendeferi et al., 2002), as a larger number of excess neurons becomes available in isometrically enlarged frontal cortices. Along the same lines, we have recently suggested that the human brain is an isometrically enlarged version of a common primate plan (Herculano-Houzel et al., 2007). This finding raises the possibility that the human species derives its cognitive advantages over other primates from a very large number of excess brain neurons, rather than from being highly encephalized. This possibility is currently under investigation.

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