Conceptual and methodological issues in comparative neuroscience & psychology: a reassessment

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Abstract

By analysing species differences in brain and behaviour, comparative neuroscience & psychology can help to understand the nature and mechanisms of behaviour. The task is enormously complex due to the number of dimensions onto which species can differ. In addition, it is shown here that the approaches, methods and concepts used in these fields contain numerous issues. Many of these issues result from the persistence of misconceptions on the evolution of brain and behaviour; despite increasing evidence that more complex approaches and concepts should be considered. Most of the issues discussed here have been presented in a previous publication (Willemet, 2013, doi: 10.3389/fpsyg.2013.00396) but have not been addressed by recent literature. They are restated here in detail, using as a reference a recent paper resulting from the cooperative work of many researchers in the field (Maclean et al. 2014, doi: 10.1073/pnas.1323533111). The factors responsible for the evolution of brain structure size are reviewed, with particular emphasis on the adjustment effect recently introduced (Willemet, 2015, doi: 10.3389/fnana.2015.00084:). The traditional interpretation of the concept of allometry is critically evaluated, and an alternative is discussed. It is also argued that the lack of consideration towards emotional, motivational and attentional factors constitutes a major obstacle to understanding the evolution of behaviour. A dataset on the neuroecology of repertoire size in songbirds is analyzed using the framework discussed here. It is concluded that until the issues detailed here are addressed, progress in our understanding of the evolution of brain and behaviour will be undermined.

Keywords: allometry, behaviour, birds, brain, brain evolution, comparative approach, comparative cognition, comparative psychology, concerted evolution, cortical evolution, encephalization, mammals, mentality, mosaic evolution, neuroecology, relative brain size, scaling rule, taxon cerebrotype, temperament

Contents

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Introduction

At the time of writing [1], the Wikipedia page on encephalization quotient (EQ) contains the following paragraph: "*Intelligence in animals is hard to establish, but the larger the brain is relative to the body, the more brain weight might be available for more complex cognitive tasks. The EQ formula, as opposed to the method of simply measuring raw brain weight or brain weight to body weight, makes for a ranking of animals that coincide better with observed complexity of behaviour.*" However, just a few lines latter the following objection can be read: "*Recent research indicates that whole brain size is a better measure of cognitive abilities than EQ for primates at least. The relationship between brain-to-body mass ratio and complexity are not alone in influencing intelligence*".

Wikipedia may not be a valid scientific reference, but these sentences pretty much sum up the current view on these issues, and most researchers would probably agree with them. What they show is how poor the understanding of such fundamental issues is, despite more than a century of research. Among the factors responsible for this situation is, of course, the intrinsic complexity of the issues related to the evolution of brain and behavior. But one of the main causes of this situation is the preconceptions and misconceptions that affect the approach, methods and hypotheses traditionally used in the field of comparative neuroscience and comparative psychology. Although these issues have been reviewed by a recent publication that simultaneously proposed an alternative framework (Willemet 2013), they still continue to affect the literature on the evolution of brain and behavior.

For this reason, a detailed analysis of the logic behind the arguments presented in Willemet 2013 is proposed here. Special focus is put on a recent paper by Maclean and collaborators (Maclean et al. 2014, thereafter Maclean et al.), which presented the unprecedented effort from laboratories worldwide to study the evolution of the capacity for self-control. The first section calls for a better integration of the affective dimension of animal behaviour. The second section examines in detail an alternative to the traditional understanding of the concept of allometry. The third section critically examines the methodology often used in comparative studies. The fourth and final section presents general comments on the comparative method, as well as an illustration of the approach advocated here.

I. The "cognition" umbrella

A. Self-control as a multidimensional character

Current comparative psychology very much focuses on species differences in cognitive abilities (Maclean et al. 2012), to a point where the terms psychology and cognition are sometimes used interchangeably (e.g. Stevens 2010). This is mainly due to the very broad definition of cognition used in comparative psychology: "cognition, broadly defined, includes perception, learning, memory and decision making, in short all ways in which animals take in information about the world through the senses, process, retain and decide to act on it" (Shettleworth 2001). Such a broad definition mixes different concepts that would better be considered separately to some extent at least (see also Cromwell and Panksepp 2011). For example, although perceptual, cognitive and motor abilities are certainly linked in many ways (as emphasized by the literature on embodied cognition, e.g. Wilson and Golonka 2013); they are distinctions between them. Cognitive abilities can be somewhat defined as the mechanisms and complexity by which an animal interprets the information from its environment; while sensory-motor abilities are primarily dedicated to acquiring the information and acting on it. Of particular interest here are the emotional (e.g. Dolcos, Iordan, and Dolcos 2011, Pessoa 2008), motivational (e.g. Padmala and Pessoa 2010) and attentional (e.g. Nieoullon 2002) factors affecting animal behaviour. Although these factors act in concert to produce behaviours, the necessity to study them separately to some extent especially appears when considering their neural bases in a comparative approach. The study of species differences in self-control illustrates this imperative.

Self-control is defined by Maclean et al. as "the ability to inhibit a prepotent but ultimately counterproductive behavior". This ability is thought to be dependent on a cognitive factor that implies the frontal cortex exercising a cognitive control over possible actions (Aron, Robbins, and Poldrack 2014). But this ability also partly depends on motivational, attentional and emotional factors (Bari and Robbins 2013). While the neural features underlying the cognitive part of self-control could potentially be approximated by the size of the brain structures implied in it (or more exactly, the number of neurons and connections), this is not neces-

[1] Encephalization quotient. (2015, March 3). In Wikipedia, The Free Encyclopedia. Retrieved 10:45, May 1, 2015, from http://en.wikipedia.org/w/index.php?title=Encephalization_quotient&oldid=649760407

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sarily the case for the neural features influencing the attentional, motivational and emotional factors implied in self-control. The reason is that these neural features include, among others, small changes in the dopaminergic and serotoninergique systems (Pine et al. 2008, Dalley and Roiser 2012). Besides, the small scale of these variations make them difficult to address in a comparative approach (see Raghanti et al. 2008).

Maclean et al. note that they used "cognitive tasks that allow valid measurement across a range of species with differing morphology, perception, and temperament" (see more on "temperament" below) and that "despite the fact that these species may vary in their reliance on vision, visual acuity, or motivation for food rewards, all species met the same pretest criteria, assuring similar proficiency with basic task demands before being tested". However, the fact that all the species tested are capable of doing the tasks and interested in doing so does not address the issue of the psychological factors determining the results.

In fact, the above indicates that the search for a single neural correlate of self-control, as done by Maclean et al., is misleading. By focusing on the "cognitive skills for self-control" (Maclean et al.), the authors fail to take into account the non-cognitive (see above for the limitations of this term) factors potentially implied in this ability. Further research needs to be done to improve the understanding of the various dimensions of self-control that are at play in the many behaviours concerned by this ability ("animals require self-control when avoiding feeding or mating in view of a higher-ranking individual, sharing food with kin, or searching for food in a new area rather than a previously rewarding foraging site", Maclean et al.). Comparative analyses can help identify some of these dimensions by testing many species in a variety of tasks involving self-control and see whether some patterns appear (some species consistently succeeding some tasks and/or failing others). In fact, the relatively weak coefficient of correlation between the two tasks used in Maclean et al. (r=0.53) suggests that at least partly different mechanisms may underlie success in these tests. Only after the dimensions of self-control are assessed will it be possible to examine the neural bases of self-control.

B. More on mentality

The discussion above highlights the need for studying the motivational, emotional and attentional factors in comparative psychology, which, although it is rarely explicitly stated, may be the main factors responsible for individual differences in personality (Denissen and Penke 2008, Corr, DeYoung, and MacNaugthon 2013) and even differences between human cultures (Han et al. 2013). The literature on animal personality often reduces the concept to its behavioural manifestations (as illustrated by the use of the term "behavioural syndrome" e.g. Sih, Bell, and Johnson 2004), with little or no reference to the mental mechanisms underlying it (but see Sih and Del Giudice 2012). Also, while some authors first suggested to study individual, populations and species levels inside a common framework (Sih, Bell, and Johnson 2004, Rale et al. 2007), it has been argued that the individual and species levels should be studied separately (Willemet 2013). This is because differences in behaviour vary along more dimensions between species than between individuals of a species (Dall and Griffith 2014, Koski 2014). Moreover, the behaviours that they affect are not necessarily comparable, as apparent in the cases of sociality (Goodson 2013).

Therefore, there is a need for a concept at the species level that could describe the motivational, emotional and attentional factors influencing species behaviour. However, despite the myriad of terms used in animal personality research (see review by Uher 2011), none of them seems particularly appropriate for describing the concept discussed here. The term "temperament" (which is used as a synonym of personality in comparative studies) has been used to describe a concept similar to the one discussed here (e.g. Byrne and Bates 2010, Herrmann et al. 2011), including by Maclean et al. themselves (see above). However, the concept of temperament as used in human research relates to the innate characteristics shaping the behaviour of an individual. Temperament thus differs from personality, the latter being supposed to be partly shaped by experience, and may therefore not act as a synonym of personality (Gosling 2008). Indeed it may be particularly interesting for comparative studies of animal personality to differentiate the physiological characteristics of the nervous system that can influence an animal behaviour from the modifications of the behaviours that arise throughout an animal mental life. In this paper, the term "mentality" is used (following Willemet 2013) because it has the advantage of emphasising that the concept describes a set of mental characteristics (and not just the behaviours that it influences), and because the term usually describes the way of thinking of a group (here, individuals from a species). Whether this term is kept or replaced by a better one or whether the concept should even stand on its own or be separated between its subcomponents has yet to be determined.

The variable sociality illustrates the need for studying mentality in comparative psychology. Indeed, as in the case of Maclean et al. study, sociality is sometimes reduced to a single variable such as group size. Yet, not only is the variable group size more complex than generally assumed (Petterson et al. 2014), but sociality also entails a number of factors others than the number of individuals in a group. Some of these factors directly depend on species cognitive abilities (the ability to keep track of previous relationships and take advantage of it for example) and others on affective factors (the propensity to search and sustain the presence of conspecifics

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or the capacity to create and sustain affective links between some of them for example). A true evaluation of social complexity would thus integrate the number of individuals in the group, but also an index of the distance of relationships between members of the group, an index of the cognitive factors at play in the organisation of the group, an evaluation of the strength of the relationship (do the individuals keep track of each other, to what extent does the relationship involve defending/helping each other, etc.) and finally an index of the quality of the relationship (does the relationship involve demonstration of affection, active search of mates, sharing of food etc.). As such, the several dimensions of social complexity are likely to be supported by different neural correlates ("pure" cognitive abilities, memory, mentality, etc.). This makes the search for a simple neural correlate of social complexity illusory and calls for more studies on the affective factors influencing animal behaviour. Consider, for example, that in some regions roe deer *Capreolus capreolus* are territorial in the summer and gregarious in the winter (Cibien et al. 1989). Roe deer did not adopt this strategy after a statistical analysis of the pros and cons of living in groups during the cold season, but most likely through selection on the mentality factors underlying this pattern; that make them tolerating other individuals and even looking for their presence during colder periods. These factors could be, as said above, subtle variations in hormones and neurotransmitters (Prendergast, Nelson, and Zucker 2002, Anacker and Beery 2013). Thus defined, the concept of mentality can be studied in a comparative approach. However, simple measures of species differences in mentality structure may be impossible to obtain, and not useful either. For example, elephants and hippopotamus are usually bolder toward other life-beings and their environment than antelopes. The differences in body weight and other body features imply that their respective lives are associated with different risks. But when considering intraspecific interactions, differences can be reversed. A hippopotamus potentially represents a greater danger to another hippopotamus than an antelope to another antelope. Such a complexity requires abandoning the notion of ranking, and instead integrating mentality inside the multidimensional space that is a species ecology.

To conclude, not only focusing almost exclusively on the cognitive aspect of behaviour prevents for a complete understanding of the behaviour in question, but consequently it also prevents an understanding of its neural bases. Thus, because they do not address the affective factors that mediate animal behaviour, Tinbergens four questions in behavioural biology, although widely accepted, appear to be a limited approach of animal behaviour (see also Bateson and Laland 2013). What is needed is a multidimensional approach of behaviour that includes the affective dimension (see also Panksepp 2011).

II. The variable "brain"

A. Absolute brain size

A.1 What is absolute brain size?

Brain size is one of the key variables in comparative psychology, mostly because of the relative ease by which data can be obtained (note, however, that even for primates, it is only recently that a relatively large dataset on brain size has been established, Isler et al. 2008). However, as discussed in Willemet, 2013, and below, there are several reasons why the variable brain size is abusively and improperly used. The first reason is the presence of consistent differences in brain constitution between taxa; at many levels of brain organization ("taxon-cerebrotypes", see Willemet 2012). Maclean et al. quickly mention these taxa specific aspects of brain organization at the neuronal level ("the number of neurons in primate brains scales isometrically with brain size [...] a scaling relationship that contrasts with other orders of animals") without realizing the consequences of it. Yet, the presence of taxon-cerebrotypes definitely prevent comparisons of various mammalian brains based on a single variable (such as brain size, brain structure size (absolute, relative or proportional), neuron number, etc.) because this variable has a different meaning for each group. Therefore, studying the evolution of neural characteristics or testing the relationship between a behavioural feature and its potential neural correlates requires a taxon-cerebrotype approach. There are no rules for finding the most appropriate taxonomic level, other than a minimum of homogeneity between the species (Willemet, 2012, 2013, see also section 4.C). Homogeneity means that the scaling of brain structures and other characters between species of a taxon follows an allometric pattern; or that the value of these features is shared by a group of species. A taxon-cerebrotype approach should therefore become the standard in comparative neurobiology (Willemet 2012). What is more; all previous studies that included species of various taxon cerebrotypes inside a common analyse should be considered as inconclusive, unless specific arguments apply to it or new analyses are done. That effectively requires reconsidering a significant proportion of the literature on comparative neuroscience & psychology.

The second reason for which brain size is a complex variable lies in its very nature. It has been emphasized (Willemet 2013) that brain size is best understood as the cumulated size of the structures that composes it, themselves being constituted by a particular number of non-neuronal and neuronal cells. Therefore, instead of considering the size of the structures being dictated by the size of the brain (as traditionally assumed by comparative neuroscientists), it is more correct to consider that it is the size of the structures that control brain

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size. Within a taxon-cerebrotype, changes in size seem to be the main way for a structure to adapt (while between taxon-cerebrotypes, there seem to be adaptations at many levels). Under this view, the concerted pattern of evolution that can be seen inside a taxon-cerebrotype is the result of two main factors. The first is non-adaptative and reflects the fact that changes in total brain size are more likely to be produced by changes in the size of large structures than changes in the size of small structures (because smaller structures have to changes size several times more than larger ones for a similar increase in brain size). The second reason is adaptative. Each structure, or group of structures, has particular functions and these functions have been more or less selected during species evolution. In this view, brains of different species have different constitutions because the size of the structures has been selected to best fit their environment (albeit under some unclear functional and developmental constraints, Willemet, 2012, 2013). What is remarkable is that, inside species within a taxon, some features are constantly the ones more selected, as they increase (or decrease) in size disproportionally compared to others (Willemet, 2013). It is therefore possible to infer to some extent the selective pressures acting on the evolution of brains inside a taxon-cerebrotype, by looking at the scaling of the brain structures, as discussed below. The impact of such reasoning on our understanding of brain evolution is far from trivial. For example, ideas such that "cortical reorganization" follows "increases in brain volume", as suggested by Maclean et al. (or that "in order to evolve a large neocortex, a species must rst evolve a large brain to support that neocortex", Dunbar and Shultz 2007b) should be taken the other way around; in the sense that it is an increase of neocortical size that (partly, since other structures enlarged as well) lead to an increase of brain size.

A.2 What causes change in absolute brain size?

The scaling of brain structures in primates is characterized by a particular enlargement of the neocortex and cerebellum (Barton 2002). This enlargement is due to an increase in non-neuronal and neuronal cell number (Gabi et al. 2010). Inside the neocortex, it is the frontal lobes that have been enlarged the most (Bush and Allman 2004), and inside the frontal lobes it seems to be the prefrontal cortex (Smaers et al. 2011). Inside the cerebellum, the lobules linked with prefrontal cortex appear to have been particularly selected (Balsters et al. 2010). All these elements suggest that the selection of neural structures in primates pervasively targeted the structures involved in cognition. In other words, a large fraction of brain size in primates reflects the investment for cognitive capacities. This is directly supported by analyses linking absolute brain size with measures of general cognitive abilities (Deaner et al. 2007, Reader, Hager, and Laland 2011).

In addition to this cognitive factor, a fraction of each brain is dedicated to what has been called the somatic factor, which corresponds to the neural mechanisms allowing control of the body. Because brain and body size are usually highly correlated, comparative neuroscientists traditionally considered, either implicitly or explicitly, the somatic factor to be the main factor determining brain size. This reasoning is not necessarily true, as discussed in more detail in the next sub-section. The somatic factor is actually a two-way street. On the one side, a larger body means larger organs that need to be innervated by more axons (e.g. Watson, Provis, and Herculano-Houzel 2012). As such, the motor cortex of a shrew might simply not have enough neurons to control a body the size of an elephant. Thus, selection for larger bodies probably necessitates a consequent enlargement of the brain structures dedicated to body control. On the other size, a larger body allows an animal to carry larger sensory organs as well as larger neural resources to process them. Selection for higher sensory-motor capacities (that enables to sample the world and to act on it) is thus a potential factor responsible for the enlargement of some parts of the brain that is related to the size of the body. And, in fact, some evidence indicates that eye size, absolute visual cortex size and visual acuity all correlate with brain and body size (de Sousa and Proulx 2014).

The degree of association between all these factors has yet to be determined (Parker and Gibson 1977, Barrett 2011, Mendoza and Merchant 2014). Moreover, other important factors having potentially played a role in structure size evolution are factors underlying physiological and psychological robustness (see Willemet, 2013). To summarize, the approach discussed here proposes that the factors behind the selection for brain structure size are either direct or indirect. Direct adaptive factors are those that directly target the mechanisms underlying the processing abilities of a structure, grossly defined. These characters under selection presumably include mechanisms permitting a structure to increase the complexity of the computation, to permit the treatment of a larger amount of information, to being more robust either physiologically or psychologically, to be quicker at performing an operation, to do a new kind of computational operation or to change the ratio between the kind of computations already existing. Alongside these direct adaptive factors, there are also indirect factors that are the necessary consequences of changes in the size of a structure. They include changes in the physiology and connectivity of a structure (Kaas 2000). Studies are needed to examine the respective roles of these factors in brain structure evolution.

Another indirect factor recently proposed (Willemet 2015) might explain at least in part (more or less important given the structure and the taxon-cerebrotype considered) why the scaling of brain structures inside a

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taxon-cerebrotype appears concerted. The logic is that the increasing size of some brain structures (due to adaptive process) might force other structures to increase their size as well (or more precisely, their number of cells and connections), even without direct selection on their functions. This adjustment effect (Willemet 2015) might be necessary for a structure to maintain its relative influence in the brain process. Otherwise, the increasing number of axons and synapses in the whole brain could possibly "dilute" too much the influence of this brain structure if it was to keep its original size. If correct, this adjustment effect hypothesis has potentially several important implications for understanding brain evolution. The first is that, depending on the structure or area, the number of neurons will not have the same signification (that is, not the same predictive power) on a structures functional capacity. For example, the fact that the olfactory bulbs in humans contain as many neurons as the largest eulipotyphlan (a mammalian order comprising, among others, shrews and moles) olfactory bulbs has been used to question the classification of humans as microsmatic (Ribeiro et al. 2014). While this may be true to some extent (see also Willemet, 2013), the hypothesis above suggests that the number of neurons in the human olfactory bulb does not represent the potential for olfactory abilities because a large part of these neurons may be there only to keep the influence of the olfactory bulb in the human brain, rather than for increasing the olfactory bulb olfactory capacity (Willemet 2015). More generally, this hypothesis helps to clarify why some species may have larger structures than others while having apparently smaller functional capacities. The second implication of this hypothesis is that it might explain part of the concerted pattern of brain evolution seen in mammalian taxon-cerebrotypes. Indeed, the enlargement of a few structures would force the others to gain more neurons as well to cope with the dilution effect. Interestingly, compared to mammalian brains, the nuclear organization of the bird brain might be less sensitive to this aspect of brain scaling. This may therefore partly explain why taxon-cerebrotypes in bird species do not seems to present the concerted pattern seen in mammalian taxa (Willemet, 2013). Much more work is needed to understand the potential consequence of this aspect of brain scaling. As discussed in section 4, however, the adjustment effect might be a major factor for understanding the evolution of brain structure size in mammals.

It is important to note that all the above does not negate the presence of developmental constraints in brain evolution. Developmental constraints influence brain evolution in at least three ways. Firstly, species are forced to evolve from the material available in the ancestral form. Secondly, not every feature can be modified. Some features are so fundamental that any changes would be unviable. Thirdly, a small number of features control the development of a much larger number of features (see review by Charvet and Striedter 2011). This implies that some features develop together and that only a few features may control much of the appearance of the brain. However, as discussed here, and although constraints are important in limiting the range of shape potentially attainable by a species, they are not the main factors that will determine the final constitution of the brain. A parallel can be made with birds beaks. By observing the allometric pattern of variation in the size and shape of the beaks in Falconiformes, one might think that bird beaks are strongly constrained by developmental constraints, or by allometric rules that would have been selected when Falconiformes branched off the bird ancestor (see below). But what about the diversity of beak forms between bird taxa? Between species of Darwins finches? And what about the beak of spoonbills for example? Such diversity precludes from assuming an overwhelming role of developmental constraints in the factors determining the size and shape of birds beaks. Similarly, Willemet (2012) noted that "the presence of various taxon cerebrotypes, the diversity of brain composition in heterogeneous taxa as well as the presence of extreme cases of mosaic evolution suggest that at least some of the developmental mechanisms controlling brain architecture in mammals have been continually under selection during mammalian evolution". Consider, also, examples such as the selective expansion of prefrontal-projecting cerebellar lobules in the primate brain (Balsters et al. 2010). The developmental constraint hypothesis would predict that this selective expansion is the consequence of a fixed pattern of brain development, but it would probably have trouble explaining why this pattern in particular exists, and why, possibly, it is not found in every other taxon cerebrotypes. Evidently, the scaling of brain features must correlate with some variables of brain development because the events happening during brain development seem to be by far the main factors responsible for determining the size and composition of the brain (other factors such as cell death appear to have a limited effect (Finlay, Darlington, and Nicastro 2001)). What the adaptative hypothesis of brain evolution discussed here suggests is that for the most part, it is not the developmental constraints that determine the pattern of brain evolution, but the selection of the brain features that determines the developmental patterns. Thus, when correlations between developmental features and brain scaling are found (e.g. Cahalane, Charvet, and Finlay 2012, Charvet and Finlay 2014), both the adaptative hypothesis and the developmental constraint hypothesis should be considered.

A.3 More on brain and allometry

If the reasoning developed here is correct, it is the end of the mosaic vs. concerted evolution binary view of brain evolution (for an overview, see Barton and Har-

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vey 2000, Finlay and Darlington 1995, Finlay, Darlington, and Nicastro 2001, Striedter 2005), which, although shown to be fundamentally flawed in Willemet, 2012, 2013, is still uncritically reported in current literature (e.g. Gutiérrez-Ibáñez et al. 2014, Lefebvre 2014, Reyes and Sherwood 2014). In fact, two misconceptions were commonly associated with this dual view of brain evolution. Firstly, the developmental constraint hypothesis of brain evolution (Finlay and Darlington 1995) has been widely considered as the one and only responsible for the concerted pattern of brain structure observed in birds and mammalian taxa (e.g. Gutiérrez-Ibáñez et al. 2014). Yet, even without referring to the adaptative hypothesis developed here, other mechanisms, such as functional constraints or size-related mechanisms (changes in brain size most likely come from changes in the larger brain structures) could explain at least part of the concerted pattern of brain structure scaling; the developmental constraint hypothesis being only one explanation among the others. Secondly, it has been suggested that adaptive changes in brain structure size due to mosaic evolution would impose "trade-offs between areas selected for different specializations in different taxa" (Lefebvre 2014). Yet, the only acceptable evidence for a trade-off between two brain regions would be to find a species or a group of species for which there is indication that the functions supported by the brain regions would be evolutionary advantageous, but that positive selection on one brain region is counterbalanced by negative selection on the other. Negative correlations are insufficient in this context and instead suggest different strategies have been selected (Willemet, 2013, see more below on the abusive use of the concept of "trade-off").

The literature just cited shows that the idea that brain size is best understood as the cumulative size of the brain structures (instead of brain structure size being determined by the size of the brain) as proposed by Willemet, 2013, has yet to be integrated. One exception is Herculano-Houzel, Manger, and Kaas 2014, who argue that: "while the use of brain size as an independent variable has useful descriptive power, it implicitly or sometimes explicitly assumes that total brain volume actually determines changes in neuronal density and even the size of various brain parts. This is obviously not the case, as total adult brain size can only be a consequence of the sizes of its component structures". However, this account is confusing. Indeed, Herculano-Houzel et al.s remark on brain evolution is not as obvious as the authors seem to believe. More specifically, later in their paper, the authors precise the following: "although using brain mass as an independent variable has great descriptive value, it wrongly implies that total brain mass also is determinant of the mass of its parts, when mechanistically it is necessarily the other way around". However, Finlay and collaborators account of brain evolution (Finlay and Darlington 1995, Finlay, Darlington, and Nicastro 2001, see also Striedter 2005), in which brain size controls brain structure size due to developmental constraints, was particularly elegant. Besides, their model provided a mechanistic (developmental) account of how the evolution of brain structures could be concerted. The idea that the size of the brain structures controls brain size; rather than the reverse, only becomes realistic (and the developmental model inappropriate) when considering the arguments behind the adaptative hypothesis presented in Willemet, 2013 and developed here, but not mentioned by Herculano-Houzel et al., 2014.

In addition, Herculano-Houzel et al.'s account of brain evolution is problematic because the authors do not consider the part of the scaling of neuron number that is adaptative. The notion of "scaling rule", which is the core concept of this recent literature (for review see Herculano-Houzel 2011) and that designates, for neural cells, "the relationship between numbers of neurons and the size (mass) of brain structures" (Herculano-Houzel, Manger, and Kaas 2014) crystallises the problem. Consider, for example, the scaling rules for the neuron number in the neocortex; a structure that can be divided in many areas with particular functions that have evolved in an adaptative fashion (Krubitzer and Seelke 2012). Given that cortical areas differ widely in size (Van Essen et al. 2012), in the number of neuron both between and within them (Collins 2011) and in their general cytoarchitecture and connectivity (Markov et al. 2014), assuming that there is a scaling rule for the neuron number in the neocortex implies that the conformation of these areas is dictated by a rule fixated early in the taxon history. In other words, speaking of scaling rule for the neocortex implies that it is the size of the neocortex that would determine the size of the areas (and hence the number of neurons), rather than the reverse (a reasoning that the authors qualified as obviously incorrect when considering the evolution of brain size, see above). There is indeed evidence for a concerted pattern of expansion of the cortical areas in primates (Chaplin et al. 2013). But this concerted pattern of evolution can be caused, as suggested here, by adaptative scaling instead of developmental or neuronal constraints only. Indeed, there is clear evidence that the size of cortical areas is not totally constrained. For example, raccoons possess a particularly large (larger than the cortical hand area in humans) cortical representation of their forepaws (Welker and Seidenstein 1959). Also, species of rodents differ widely in their cortical organization, and these differences can be linked with lifestyle and ecological variables (Krubitzer, Campi, and Cooke 2011).

More specifically, Herculano-Houzel et al. (2014) assume that the diversity of brain size and composition in mammals can be explained by "clade-specic mosaic evolution in a context of otherwise concerted scaling". They propose, for example, that primates "have branched off the mammalian ancestor with step changes that in-

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creased the rate at which numbers of neurons increase with body mass [...], and caused increased NCX/NROB and NCB/[N]ROB ratios as the rest of brain gained neurons in evolution" (brackets added, NCX, NCB and NROB: numbers of neurons in the cerebral cortex, cerebellum and rest of brain (brain size minus the size of the neocortex and cerebellum), respectively). Assuming that the mosaic adaptations selected during the emergence of a taxon will become the rules that determine the concerted evolution of the characters inside this taxon raises two related conceptual difficulties. The first difficulty consists of knowing why the ability to adapt (to break "rules") would have been limited to some privileged, founding species. New forms of mammals presumably emerged when the selection pressures acting on them took a new direction compared to the ancestral mammals. Thus the reason why the descendants species maintain some kind of distinctive characteristics (which for brain characters in mammals are reunited under the concept of taxon cerebrotypes), is that the direction of the selection pressures is sensibly the same in these species as it was for the ancestral form. This is adaptation. The second difficulty is to explain how a rule could have been selected during evolution. Stevens 2009, for example, suggested that "presumably, any conserved pattern-formation mechanism has been selected because it permitted the existence of allometric relations so that one mechanism would work for an individual of any size". However, a character cannot be selected in advance, and thus the selection must occur in each species. This is again adaptation.

Descendant species exploit the innovations of their ancestors. Primate innovations, for example, include packing a large number of neurons into a limited space (Herculano-Houzel et al., 2014). But speaking of rule is not necessarily justified, because the reasons why current primate species have kept these innovations are similar to the reasons why the ancestral species evolved them in the first place. More generally, and although each variable is particular, the idea that allometric patterns can sometimes result from directional selection, instead of developmental and functional constraints only, is gaining momentum in evolutionary biology literature (Plabon et al. 2014, see Newell 1949 for an early account, and Gayon 2000 for an historical review of the concept of allometry). Indeed, the framework above suggests that brain evolution is best understood when considering that the allometric patterns of brain evolution (including the allometric relationship between brain and body size) can result from adaptative selection acting above developmental and functional constraints on each species and at every moment of their evolution, as long as the direction of selection is shared between species. This account diametrically differs from the traditional interpretation of allometry (see Willemet 2013 for additional evidence) and has potentially far reaching implications for our understanding of brain evolution.

B. Relative brain size

In line with the traditional approach of comparative psychology (e.g. Lefebvre, Reader, and Sol 2004), Maclean et al. put great emphasis on the variable relative brain size and test it as a potential proximate mechanism underlying self-control. Yet, as detailed below, the variable relative brain size has an uneven value and a complexity far beyond what is generally considered (see Willemet, 2013), challenging the "common use of relative brain volume as a proxy for cognition" mentioned by Maclean et al.

B.1 What is relative brain size?

Relative brain size is a variable corresponding to the residuals from a linear regression of the logarithmic values of brain mass onto body mass. Both variables are problematic. On the one side, body weight is highly dependent on the amount of fat, muscle, and viscera in the body, all of which are differently innervated. On the other side, brain weight is, as seen above, determined by the weight of the brain structures, and the proportions of these brain structures vary with brain size. It is possible to examine the problem of using relative brain size by considering two hypothetical taxa A and B. Species in taxon A have consistently larger brain size than species B for similar body size. Species in taxon A also have a relatively large part of their brain dedicated to cognitive abilities, whereas the brains of species in taxon B are mostly dedicated to somatic and/or sensorial and/or robustness functions (see above). Both taxa show a fairly strong correlation between the size of their brain and the size of their body. What does relative brain size represent in these taxa? To answer this question it is first necessary to understand what causes changes in relative brain size. This is unlikely to be selection for a larger hippocampus, or any other relatively small structures, because the size of the hippocampus is so small that it would need several folds variations in hippocampus size before having a significant variation in brain size. Therefore, in both taxa, changes in relative brain size most likely come from size variations of big structures, mostly neocortex and cerebellum (see section 4 in Willemet, 2013).

Moreover, the regression line of brain size onto body size at the log scale cannot represent the part of the brain dedicated to body control (figure 1.a.), because even species with values below the regression line must be able to scan and evaluate their environment to produce behaviours. Thus in all taxa, each species already has more processing capacities than those required to control their body (figure 1.b.). In fact, in taxa A, the somatic factor represents a part so negligible of the brain's processing capability that relative brain size does not noticeably change the fraction of the body factor enough to

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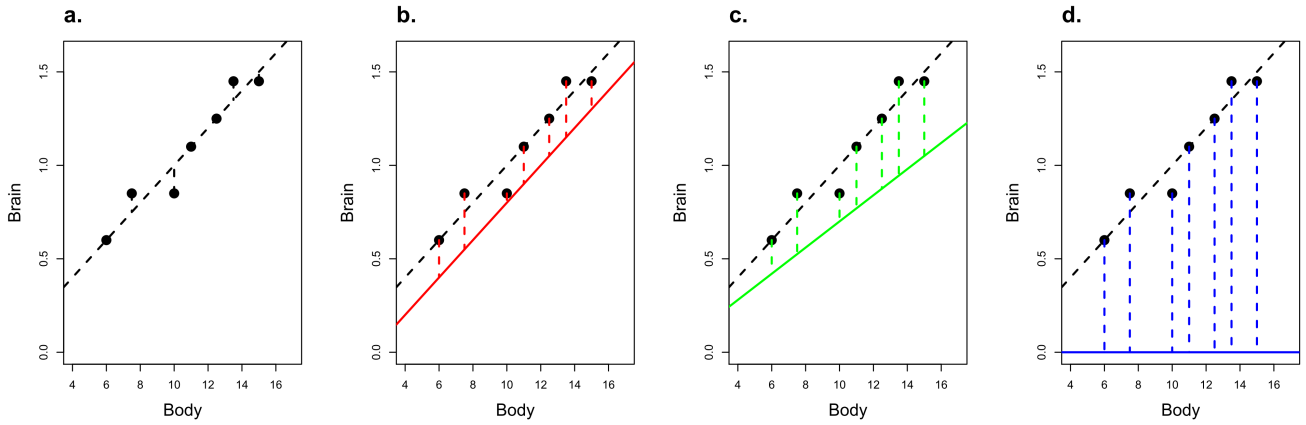

Figure 1: *Relative brain size and cognitive abilities. (a) Residuals obtained by the regression of brain onto body size. This method assumes that most of the increase in brain size is due to body size, with the variations of residual brain size correlating with species cognitive abilities. (b) In this model the intercept of the slope has been reduced. In practise this does not affect the relative values of the residuals, but in theory these residuals are more realistic than those obtained in (a). This is because this method takes into account the obligatory fraction of brain size that is not directly related to the body factor, but the cognitive factors that allow an animal to behave and react to its environment. (c) Here the slope has been reduced compared to (a). Changing the slope permits to take into account the part of brain enlargement that is an adaptation to a cognitive factor. (d) This last model is the extreme of model (c), in which the majority of brain size has evolved in response to selection on factors other than the somatic factors, and in particular selection on cognitive abilities. In these taxa, absolute brain size correlates better with cognitive abilities than residual (relative) brain size.*

give any indication of the processing capacity of the brain dedicated to cognitive functions. In taxa B, changes in relative brain size may give more indication on possible selection for more processing capacity dedicated to cognition. But in both cases, it is true only if the common factor underlying the variation in relative brain size is selection for increased processing capacity (instead of selection for sensory abilities or motor control for example). One possibility for understanding the part of brain size that is dedicated to cognition is to examine, within species of a taxon-cerebrotype, the relationship between a measure of species differences in cognitive abilities and the residuals of a regression of brain onto body size, while varying the value of the slope (see Willemet 2013). In primates (whose characteristics are comparable to the species in taxon A), the cognitive factor seems to represent the factor determining most of brain structure sizes, as determined by the fact that brain size (slope =0, figure 1.d.) best predict a measure of cognitive abilities that any other residuals. Although no such measure exists in felids yet; a tiger does not appear to behave with much more complexity than a wildcat with a much smaller brain for example (suggesting that they have characteristics comparable to the species in taxon B). This suggests that the fraction of the absolute brain size dedicated to cognitive abilities decreases with brain size in felids and that most of the increase in brain size is due to the body factor, sensory-motor capacities or other non-cognitive factors. Therefore, in the hypothesis that some felid species have enlarged parts of their brain in response to a need for larger cognitive capacities, it might be expected that residuals from a slope equals to (figure 1.b.) or close to (figure 1.c.) the slope of a regression of brain onto body size are more related to differences in cognitive abilities than are absolute brain size. To make things even more complex, it should be noted that residuals do not have the same value along the range of brain size, since similar residuals can represent different brain composition and different values of neurons (Herculano-Houzel, 2007). Moreover, by examining relative brain size, we assume that it is the brain that varies adaptively, and that body size is fixed, whereas in many cases the opposite may be true (Deacon 1990). However, phylogenetic methods have been developed to address this last point (Montgomery et al. 2010).

Following the framework discussed above, and although this level of analysis is commonly disregarded (e.g. Shultz and Dunbar 2010) because of the suggestion by Pagel and Harvey 1988, that at least part of it could be explained by sampling error, there is potentially significant information to be found in the relationships between brain and body size between phylogenetic levels. The allometric coefficients and the strength of the relationship (as estimated by the coefficient of determination for example) between brain and body size within a genus might give insight into the relative importance of the body factor within the brain inside a genus for example.

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B.2 Confusion in the terms and methods

The discussion above suggests that the variable relative brain size has an uneven biological value as a proximate mechanism underlying species differences in cognitive abilities. In top of that, the literature on this subject is affected by a confusion of terms. The term encephalization" has been used to define "a species' deviation from some observed or expected relation between brain mass and body mass in a reference group" (Harvey and Krebs 1990). As such, the term "encephalization" is similar to "relative brain size" or "brain size residuals". This definition was based on the assumption (wrong, as discussed above) that absolute brain size was not truly adaptative, being mainly a consequence of body size. Moreover, over the years, the term encephalization has been used to design a diversity of neuroanatomical measures, including measures that do not take body size into account (Lefebvre 2012). For sake of clarity, therefore, the past concept behind the term "encephalization" (i.e. relative brain size) should probably be called "relative encephalization", and the term "absolute encephalization", or simply "encephalization" should be reserved for absolute brain size. Similarly, expressions such as "large brains", "larger brains" or "enlarged brains" designate absolutely large/larger brains. If used to design the size of the brain relative to the size of the body (e.g. Lefebvre and Sol 2008), then the term "relatively" should be systematically added. The term evolutionary encephalization would thus designate the increase in absolute brain size that occurred during vertebrate evolution (Jerison 1973). Removing this confusion of terms is fundamental for comparative psychology.

The confusion lies not only in the terms but also in the methods. Indeed, in a review of the methods used to examine the neural level that best predicts cognitive abilities in mammals, Deaner, Nunn, and van Schaik 2000, concluded that, at that time, there was "no theoretical or empirical basis for preferring any of the methods examined here". As it appears in a recent review of primate encephalization literature (Lefebvre 2012), the confusion continues today. In fact, most authors today report supposed evidence for a role of both absolute and relative brain size in explaining absolute cognitive abilities (e.g. Maclean et al., Stevens 2014); despite the fact that the two variables are uncorrelated. The framework above offers some theoretical justification for removing this confusion.

For example, the study from Reader and Laland 2002 has been taken as evidence for a link between relative brain size and cognition (e.g. Lefebvre, Reader, and Sol 2004, Shultz and Dunbar 2010). However, the methods used by Reader and Laland (2002) do not support this conclusion (and see Reader, Hager, and Laland 2011). Indeed, Reader and Laland (2002) did not use body mass because of concern about measurement error, and instead used the size of the brainstem (cumulated size of the mesencephalon and medulla oblongata). The two variables found by Reader and Laland (2002) to correlate with innovation are the absolute size if the "executive brain" (defined as the sum of the neocortex and striatum), and the ratio of the size of the executive brain onto the size of the medulla ("executive brain ratio"). The "executive brain" size and "executive brain ratio" are correlated between each others and with absolute brain size in primates (figure 2.a.b.c). This is not surprising, since most of brain enlargement in primates is due to an enlargement of the neocortex in particular. As such, these methods are expected to have sensibly the same capacity to predict measures of cognition in primates (based on social learning, innovation, and tool use frequencies), because, as seen above, a large fraction of the size of the primate brain appears to be dedicated to cognitive functions. The measure that does not correlate with innovation is the residuals from a regression on the "executive brain" onto the medulla size. In fact, "executive brain" residuals do not correlate with absolute brain size (figure 2.d). The residuals obtained by such method quantify the difference between the size of the neocortex and striatum and the size expected given the allometry between these two structures and the size of the brainstem (medulla and mesencephalon). A large fraction of the size of the brainstem is likely to be determined by the size of the spinal cord and thus by the size of the body. In contrast, most of the size of the neocortex in particular may be relatively independent from the size of the body, at least in primates. Because of the relative size of the neocortex in the primate brain, what the "executive brain" residuals measure, therefore, is likely to be related to what relative brain size represents. And indeed, these two variables may be correlated (figure 2.e. and see Willemet, 2013). Although more precision in the measurements of the neuroanatomical variables (especially brain and body size) might improve this relationship, there are several reasons why these two methods cannot give exact same results, including the fact that body mass is not the only and even best approximation of a body size factor (measures based on the spinal cord are likely to be more precise), and that relative brain size does not consider which of brain structures or body size has been selected. Nevertheless, and to the extent that innovation is correlated with species cognitive abilities, the discussion above helps to understand why "executive brain" residuals did not correlate with the cognitive measures tested by Reader and Laland (2002). This is because by removing the allometric relationship between the structures, the executive brain residuals also remove the size factor of the brain structures, which is largely correlated with a structures processing capacity in primates.

The executive brain residuals and executive brain ratio are two examples (b and c, see below) among the three methods examined by Deaner, Nunn, and van Schaik

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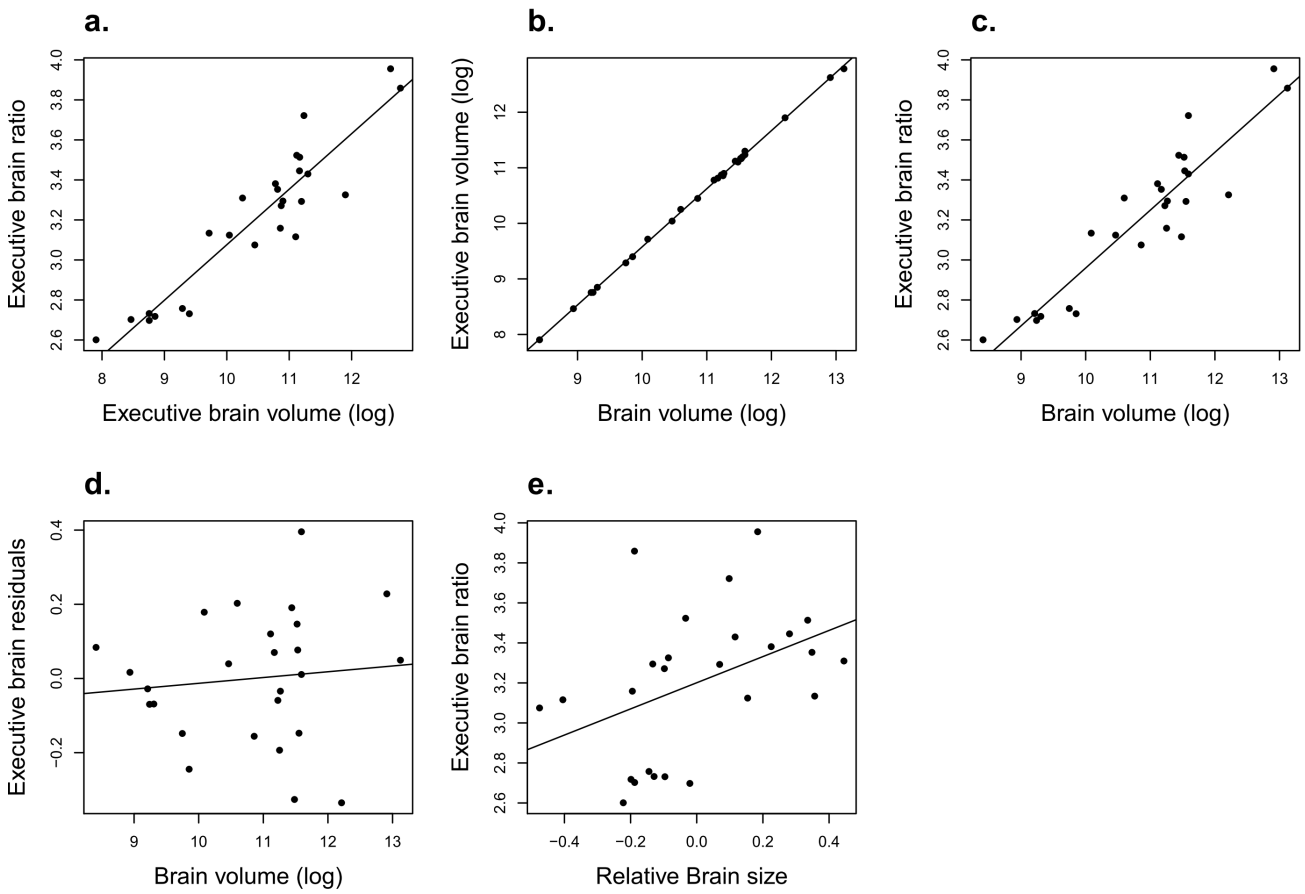

Figure 2: *Executive brain (neocortex and striatum, Reader and Laland, 2002) and brain volume in simians. (a) Executive brain ratio (log) onto executive brain (log). Person correlation test: t = 12.3044, df = 24, p-value <0.001, cor = 0.93. (b) Executive brain (log) onto brain volume (log). Person correlation test: t = 215.2337, df = 24, p-value <0.001, cor = 1. (c) Executive brain ratio (log) onto brain volume (log). Pearson correlation test: t = 11.9745, df = 24, p-value <0.001, cor= 0.93. (d) Executive brain residual onto brain volume (log). Pearson correlation test: t = 0.5189, df = 24, p-value = 0.6086, cor=0.11. (e) Executive brain ratio (log) onto relative brain size. Pearson correlation test: t = 2.2815, df = 24, p-value = 0.03168, cor=0.42. Data from Stephan, Frahm, and Baron 1981.*

2000. Precisely, Deaner et al. used (a) the residuals from an interspecic regression of non-V1 neocortex onto body mass, (b) the residuals from an interspecic regression of non-V1 neocortex onto the size of the brain minus the size of the neocortex and (c) the ratios of the non-V1 neocortex to the size of the brain minus the size of the neocortex. Deaner et al. did not test absolute values because their assumption was that the "neural traffic"; that is, the part of brain size supposedly due to body size, needed to be factored out. As it can be expected from the discussion above, the variables used by Deaner et al. (2000) correlate with absolute (c) or relative (a, b) brain size (figure 3). Note however, that the correlation between the residuals obtained by method b and encephalization quotient is low. This is not surprising given that, as shown above, the variable relative brain size is problematic in many respects. So where to go from there? Does it help to analyze the structure individually? If so, what method should be used? What is the best measure that correlates with cognitive abilities? A preliminary framework is described in subsection 4.

B.3 Examination of the support for using relative brain size

Other than the relative ease by which datasets on brain and body size can be constructed, one reason why relative brain size raised so much interest is that significant relationships have been reported between relative brain size and a number of ecological or behavioural variables. A closer examination, however, reveals that most of these studies are not interpretable the way they traditionally are. Indeed, with the above in mind, it is possible to examine the references cited by Maclean et al. and which suggest that relative encephalization correlates with species cognitive abilities.

The first reference is the influential book from Jerison 1973: "Evolution of the Brain and Intelligence". As

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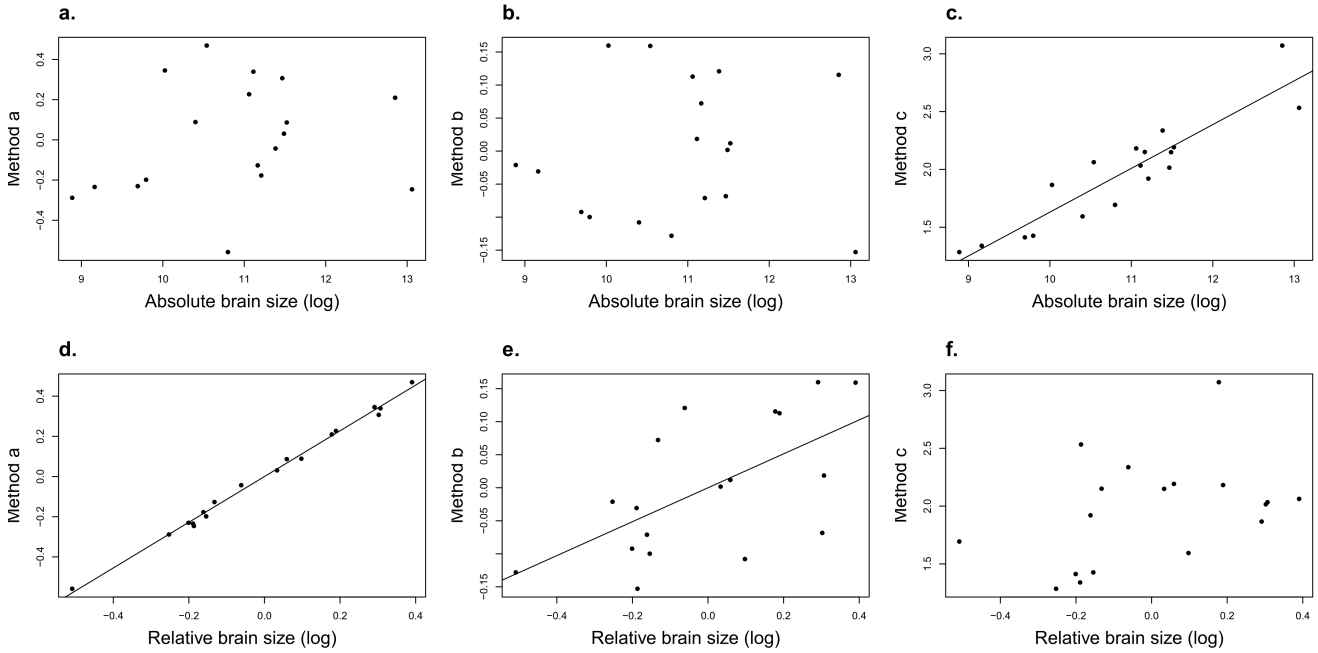

Figure 3: *Correlation between methods (a) taking the residuals from an interspecic regression of non-V1 neocortex onto body mass, (b) taking the residuals from an interspecic regression of non-V1 neocortex onto the size of the brain minus the size of the neocortex and (c) taking the ratios of the non-V1 neocortex to the size of the brain minus the size of the neocortex and absolute and relative brain size. Pearson correlation test between absolute brain size and method a: t = 0.8985, df = 16, p-value = 0.3822, cor = 0.22, method b: t = 0.2693, df = 16, p-value = 0.7911, cor = 0.07, method c: t = 9.365, df = 16, p-value <0.001, cor = 0.92. Pearson correlation test between relative brain size and method a: t = 53.8779, df = 16, p-value <0.001, cor = 1, method b: t = 3.0864, df = 16, p-value = 0.007079, cor=0.61, method c: t = 1.7096, df = 16, p-value = 0.1067, cor = 0.39. Data from Barton 1998.*

noted here and in Willemet, 2013, there are serious problems with this account of brain evolution; including the mixing of taxa and the false assumption that body size is consistently the main factor controlling brain size.

The second citation is Kappelman 1996: "The evolution of body mass and relative brain size in fossil hominids", which suggests that the large relative brain size of human is partly due to a recent reduction of body size during human evolution. As such, it does not provide direct support for a role of relative encephalization in cognitive abilities.

The rest of the citations concern works that have found positive relationships between a measure of relative brain size with an estimate of the success of bird (Sol et al. 2005) and mammal (Sol et al. 2008) species introduced into novel environments, as well as a review by Lefebvre, Reader, and Sol 2004, on the literature on brain size and an estimate of behavioural innovation. These results and others have been widely understood as evidence that "a large brain [relative to body size] facilitates the construction of novel and altered behavioural patterns and that this ability helps dealing with new ecological challenges more successfully" (Sol 2009, brackets added). It is important to get a more nuanced view of these results. Indeed, at the behavioural level, both the capacity to settle in new environments and the propensity for innovative behaviours do not only depend on animal cognitive abilities, but also on mentality factors (Greenberg and Mettke-Hofmann 2001). As said above, the neural basis of these mentality factors are unlikely to be found at the level of brain structure size, let alone at the (absolute and relative) brain size level. But the point here is that these studies often mix different taxa in their analyses, or, due to a lack of data, they even analyse taxa instead of species. Yet because the variables analysed have different values between taxa, this kind of analysis is only able to describe tendencies between species of a class, or between taxa, and cannot indicate the causal relationship between two variables. In other words, the correlations found at these levels of analyses, though interesting, cannot be extrapolated as being the mechanistic bases of the behaviours tested.

Maclean et al. asked "why might absolutely larger brains confer greater cognitive advantages than relatively larger brains". To conclude on the issues discussed since the beginning of section two; the answer given above is that this is differentially true given the taxa, and that this depends on the importance of the quantity of processing capacity added with relatively larger brain over that present with absolute brain size. In all cases, evolutionary changes in relative brain size are either due to variations of body mass, or the increase (or

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decrease) or certain brain structures. Relative brain size is thus better understood as a consequence of adaptative changes in brain structure sizes, rather than, as considered by Smaers and Soligo 2013, a factor of neural variation. Thus, despite its acceptation in comparative neuroscience, the idea that relative brain size is a proximate "mechanism supporting cognitive evolution" (Maclean et al.) is mostly based on weak empirical and theoretical evidence. This is not to say that relative brain size is not a potentially important variable when it comes to the evolution of cognitive abilities. But this issue has to be examined inside a taxon-cerebrotype approach with careful use of the methods discussed above, and with appropriate anatomical and behavioural data. In all cases, the widespread idea that the so-called "allometric effect" of body size must be systematically remove before any analysis in brain studies appears false on many grounds.

B.4 The case of trade-offs

Selection pressures often act in different directions. For example, selection for a shorter time of development and selection for a larger body size supposedly act against each other, because a longer time of development is necessary for growing a larger body. Hence, the selection for larger brain structures has certainly been subject to evolutionary pressures acting against an increase of brain size. This is by extending this logic that the scaling of brain and body size has traditionally been thought to be due to tradeoffs with ecological and lifestyle variables. In particular, a lot of interest has been put into finding the variable that would best correlate with relative brain size (e.g. Navarrete, van Schaik, and Isler 2011, Potts 2011). Such analyses are likely to be limited, however, because of the number of variables implied in brain and body size scaling. Moreover, the field has been largely victim of using multi-taxa analyses; leading to spurious relationships (the relationships were not between species but between taxa). There are signs that the field is now moving toward a taxon-centred, multidimensional analyses of the evolution of brain size with regards to the other variables (Isler and van Schaik 2014). However, there are still significant issues that need to be addressed.

First, most studies on the supposed evolutionary correlates of brain size are interested in explaining "the evolution of larger brains relative to the overall trend with body size" (Isler and van Schaik 2014). One assumption behind this approach is that the strength of the pressures and constraints acting on brain and body size are comparable along the range of brain and body size. This is unlikely, and thus the values of the residuals probably differ along the range of brain and body size. Moreover, instead of focusing on the residuals only, important knowledge could probably be gained on the mechanisms of brain/body scaling by comparing the coefficients of the allometric relationships between taxa.

Another issue is that most ecological and lifestyle variables correlate both with body and brain size, causing issues of multicolinearity. Many studies analyze the relationship between brain size and ecological and lifestyle variables using residuals or multiples regressions (e.g. Barrickman et al. 2008). Yet, the more a variable correlates with brain size, the more the relative size of this variable when regressed onto body size correlates with relative brain size. Therefore, it is likely that some correlations found between relative brain size and other variable relative to body size are more representative of the correlations between absolute brain size and the absolute values of these variables rather than representative of the relationships between these variables and relative brain size. This can be problematic if these variables are then compared to variables that correlate more with body size than brain size.

Another potential issue with the literature examined here is the almost ubiquitous use of the concept of "trade-off". As an emblematic example, Isler and van Schaik 2014 note that the "expensive Tissue Hypothesis [which] suggests an energetic tradeoff between brain tissue and the size of the digestive tract [...] may still explain the special case of humans as compared to great apes" (brackets added). As said above, however, a trade off only exists when the two variables implied would benefit from being selected. In other words, constraints alone are not sufficient for trade-offs to exist, since there must also be evolutionary pressures acting on the two variables. Unless evidence that having a larger intestine would be beneficial to the human species, or would have been in some time in the past, there is no need to invoke the notion of trade off in this particular case (and see Hladik, Chivers, and Pasquet 1999).

More generally, there is a widespread assumption that every species would need what we, humans, think is advantageous. Isler and van Schaik (2014) for example, ask: "would not most primates, or indeed animals generally, benefit from being smarter if there were no countervailing costs of evolving larger brains?". While this idea seems globally appealing from a human point of view, it is in fact highly biased. Not all species need to be the smartest, strongest, fastest, etc. There is room for species with simple but quick understanding of the environment, and this is why there are species with simple brains. There is room for species with more complex understanding of the environment, and this is why there are species with complex brains. The assumption behind the trade-off approach; that all species want to get more but that only some can afford needs to be reconsidered.

Another problem is the difficulty in considering all the variables potentially responsible for the pattern observed. For example, van Woerden, van Schaik, and Isler 2014 argued that they found support both for the expensive brain hypothesis (Isler and van Schaik 2009) and the cognitive buffer hypothesis (Sol 2009). Unlike many studies that examined groups of heterogeneous species,

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van Woerden et al. restricted their analyses to primates, even further dividing the primates in Platyrrhini, Catarrhini and Lemuriformes. If we focus on the cognitive buffer hypothesis, van Worden et al. consider a significant correlation between, on one side, the difference between the coefficient of variation of a measure of diet quality and the coefficient of variation of a measure of environmental seasonality and on the other side, relative brain size, as a confirmation of the cognitive buffer hypothesis. The cognitive buffer hypothesis states that species with relatively larger brain would have more cognitive abilities to deal with a complex environment (Sol 2009). By their very nature, however, the analyses carried out by van Woerden et al. cannot "confirm" nor infirm the cognitive buffer hypothesis. This is because they rely on indirect estimate of the species ability to cognitively adapt to their environment. In fact, the reason why the cognitive buffer hypothesis considers the relative size of the brain to be of adaptative value is that absolute brain size has traditionally been considered as a non-adaptative consequence of body size. As such, findings such as fruit-eating species having relatively larger brains than leave-eating species have been interpreted with the following reasoning: "individual species of fruits are more distributed and available for a shorter periods than are leaves, thus requiring larger home ranges as well as the ability to predict when food patches can be found" (Mars et al. 2014). Yet not only there are now reasons to suspect that body size is not the main factor controlling brain size, at least in primates (see above), but studies using direct estimates of cognitive abilities in primates have reported a link between cognitive abilities and absolute, not relative, brain size (Deaner et al. 2007, Reader, Hager, and Laland 2011, and see above for concordant evidence at the structure size level). In contrast, there is no direct support for the cognitive buffer hypothesis. Direct evidence would include the demonstration that, for example, the ability to switch between resources, to deal with exceptional situations, to remember food places and predict the availability of others, to take optimal decisions in term of resource managing would be correlated with relative brain size. Thus, van Woerden et al. 2014's interesting results open more questions than they answer. Note that for brains of rather similar size, the framework above does predict that, species specific adaptations aside, the cognitive advantages should go to the species with relatively larger brains. This is because in these species the somatic factor should be even smaller.

More generally, while most authors agree that there are many ways for a species to adapt to the selection pressures acting on brain and body size; most of the research has been aimed at finding a single way. Yet, the fact that species within a taxon may differ in the strategy they followed means that any analysis trying to examine a single main strategy may be fundamentally flawed. Sayers 2013, lucidly noted that "questions of [...] primate evolution more generally cannot be answered by the frequent approach of broad characterizations, categorization models, crude variables, weakly correlative evidence, and subjective definitions". As such, understanding particular aspects of brain evolution in relation to ecological and lifestyle variable (and even some psychological abilities, as seen here in the study of Maclean et al.) may be possible only by finding common patterns between individual or group of species having responded to a certain set of selection pressures. Alternative methods, potentially more sensitive than the use of residuals, include methods of machine learning such as artificial neural networks. Because all of this requires high-quality data; data collection must become a top priority in comparative studies.

B.5 Other points

1) The presence of taxon-cerebrotypes affects all levels of analysis in brain studies. This includes studies of the genetic basis of brain size evolution in mammals, a topic that is receiving increasing attention (e.g. Enard 2014, Montgomery and Mundy 2014). In view of the elements discussed in the sub-section 2.2, the problem is exacerbated when looking for genomic correlate of relative brain size (e.g. Gutierrez et al. 2011, Castillo-Morales et al. 2014).

2) Despite its historical value in comparative psychology, Jerison's universal encephalization quotient (tested by Maclean et al.) should probably be abandoned; since it cumulates many of the issues discussed above (see also Willemet, 2013). Some of the widespread ideas that it contributed to disseminate, such that carnivores outsmart their prey based on their relatively larger brains should therefore be put to an end (note that a more recent claim (Shultz and Dunbar 2006) about a bias in predation toward species with relatively smaller brains (taken as evidence of more effective anti-predation behaviours from those species with relatively large brains) is problematic because it confounds the different taxa in calculating the brain size residuals).

3) The work at the cellular level has revealed that changes in the size and number of neurons inside a structure do not follow a simple relationship. In particular, while primate species with larger brains have evolved a larger neocortex relative to the size of the cerebellum (Barton 2002), the ratio between their number of neuron appears to have remained constant (Herculano-Houzel 2010). Also, there are discrepancies between the rates at which the neocortex and olfactory bulb gained mass in insectivores and glires compared to the rates at which these structures gained neurons (Ribeiro et al. 2014). These results corroborate the adaptative approach discussed here, while emphasising the need for finer analyses since structure size can exaggerate the actual selection on the number of neurons. In fact, even the number of neurons inside a structure is a gross approximation of its

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processing power, since the density of neurons is not homogeneous throughout a structure volume (Collins 2011) and since the number, layout and nature of connection between neurons may be as important as the number and nature of neurons (hence the difference between brain areas).

4) Comparative biology traditionally groups prosimians and simians species into a primate taxon. There are indications, however, that these two groups should probably be analysed separately in brain studies (Willemet, 2012).

5) Maclean et al. include dogs in their analyses. Because the brain supports other functions that cognitive ones, and that some of these functions may have been rendered unnecessary (or were influencing characters not researched) during domestication; domestic and wild forms should not be included in comparative studies of brain and cognition (Willemet, 2013).

III. Statistical significance and biological significance

Statistical analyses only give mathematical descriptors of the relationships between the available values of the variables. The main difficulty, therefore, is to evaluate whether the analysis and the results are meaningful in a *biological* way (Willemet 2013).

A. Discussion of Maclean et al. analyses

Besides the common difficulty in interpreting the statistical coefficients of the methods commonly used (e.g. Lecoutre, Lecoutre, and Poitevineau 2001), comparative studies face another difficulty, namely that the species that they include in the analyses must be comparable. In this regard, the first analysis of Maclean et al. (figure 2 in Maclean et al. paper) has a limited biological interest for analysing the neural basis of self-control. The main reason is that mixing different mammalian taxon-cerebrotypes gives flawed results (a 10 grams carnivore brain does not have the same constitution and therefore not the same processing capacities as a 10 grams rodent brain for example). Even more dramatically, the authors analyzed bird species alongside mammalian species in their analysis, even though simultaneously analyzing different vertebrate taxa considerably amplifies the problems just described between mammalian taxa. The outcome of such analysis is, at best, only a tendency between variables and not a proper indication of the relationship between them.

The second analysis (figure 3 in Maclean et al. paper) restricted to primate species is more adequate. Following classical interpretation of such analyses in comparative psychology, Maclean et al. note that "absolute brain volume was the best predictor of performance across tasks and explained substantial variation across species (r = 0.550.68)". In order to show that one variable explains another, it is necessary to find convincing evidence that change in one variable change the other in a way that is biologically significant. No such evidence can be found in Maclean et al.s results, which only show that in general primates that have a higher composite score also have larger brains. Maclean et al.s analysis includes less than ten percent of the total number of primate species, and thus there is the possibility that including more species could precise or modify the conclusion. Nevertheless, there are indeed many reasons to expect that brain size does have an impact on self-control in primates, in particular via an increase in absolute and relative size of the frontal and prefrontal cortex.

Importantly, the part of the composite score uncorrelated with brain size may in fact be determined by the mentality factor defined above. As such, the ability for self-control in primates could be correlated with the ecological factors to which the ability for self-control matters most. It is interesting, therefore, that Maclean et al. analysed the correlation between a number of ecological factors and the composite measure of self-control. In particular, the authors tested the relationship between dietary breadth and self-control in two analyses.

The first analysis is a regression of self-control scores onto a measure of dietary breadth. In view of the results (R=0.68), the authors concluded that "dietary breadth is strongly related to levels of self-control". Yet, the data given by Maclean et al. shows that at least two species of lemurs have levels of dietary breadth equal to or superior to most great ape species, despite lemurs having low composite scores of self-control; in fact lower than the estimate for the ancestral primate species. Thus, despite the significant statistical relationship between dietary breadth and self-control, its biological signification remains to be precisely evaluated.

In the next analysis, the authors sought to "provide an integrated test of variance explained by absolute brain volume and dietary breadth" by using a multiple regression analysis. They found that "this model explained 82% of variance in performance between species with significant and positive coefficients for both absolute ECV and dietary breadth, controlling for the effects of one another". Maclean et al., concluded that "while correlated with one another (t = 3.04, P <0.01, = 0, r = 0.32), both brain volume and dietary complexity account for unique components of variance in primate cognition, together explaining the majority of interspecific variation on these tasks. In this model the independent effect for dietary breadth (r = 0.45) was comparable to that for ECV (r = 0.49)". Yet (and it echoes what has been said above), if brain size is "the major proximate mechanism underlying the evolution of self-control", as Maclean et al. put

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it, how can another variable explain independently that much variance? Unlike brain size, dietary breadth cannot be a causal mechanism controlling self-control. Indeed, the independent effect of dietary breadth on self-control could be an estimate of some of the mentality factors influencing self-control that are independent of brain size. It is plausible, in such a way that more dietary breadth needs more self-control; or inversely, more self-control allows for more dietary breadth (as stated by Maclean et al. "individuals with the most cognitive flexibility may be most likely to explore and exploit new dietary resources or methods of food acquisition"). This view does not contradict Maclean et al.s suggestion that "dietary breadth acts both as a selective pressure and a metabolic facilitator of cognitive evolution". But it also encourages to search for other factors, having selected for self-control via other means that selection of brain structure size (and therefore on brain size); that is, having selected for the mentality factors implied in self-control. Maclean et al. observed that "animals require self-control when avoiding feeding or mating in view of a higher-ranking individual, sharing food with kin, or searching for food in a new area rather than a previously rewarding foraging site". This should prompt searching for mating system, bonding system and other ecological and social factors having potentially selected for the various dimensions of self-control.

The proposal that these analyses "implicate robust evolutionary relationships between dietary breadth, absolute brain volume, and self-control" (Maclean et al.) should therefore be put into perspective because, as reviewed above, several dimensions of complexity have not been taken into account. This warns against directly going from a statistical relationship to a biological relationship.

B. Other points

1. For a relationship to have any biological sense, variation in one variable should directly or indirectly (through the effects of another variable) affect the other variable(s) in a way that is biologically significant for the species. Often, however, the relationship will be affected by outliers. Maclean et al note that they "inspected all phylogenetic generalized least squares (PGLS) models for outliers, defined as species with a studentized phylogenetic residual value of >3. There were no outliers in any statistical models according to this criterion". Such criterion is purely statistic. The biological interpretation of an outlier is an individual (or a species) for which the relationship of interest does not seem to apply even if it applies for the group in general. Outliers, far from diminishing the importance of a relationship, often can bring insight into other mechanisms playing a role in the relationship of interest. Finding outliers can be therefore as important as understanding the relationships between the variables of interest. This requires that the relationship studied is strong and reliable. At least five factors influence the reliability of such an analysis. The first factor is the number of species. In Maclean et al.'s study, composite scores are available for only fifteen primate species. While this is already a lot considering the current standard of comparative psychology, this is obviously too low to obtain a clear understanding of the relationships that exist between the more than two hundred species of primates. Secondly, the choice of species is primordial. There are a lot of apes and lemurs in Maclean et al.'s dataset, but relatively few monkey species (and see above about the hazard of mixing strepsirrhines and haplorhines species). This potentially skewed the analyses. The third one is the quality of the variable. Mixing different methods, different datasets, using low quality samples, not enough individuals in a sample or a biased sample of individuals are factors that directly affect the analysis. Maclean et al. study is a large step forward in this respect. The fourth one is the nature of the variables. The composite score used by Maclean does not allow distinguishing the dimensions of self-control (see section 1). Finally, the fifth factor is the need for multidimensional analyses, which take into account other variables known to act on a variable of interest. The number of variables that can be included in a multivariate analysis directly depends on the number of species for which data is available.

2. Maclean et al. conclude from a review of the literature that "with respect to selective pressures, both social and dietary complexities have been proposed as ultimate causes of cognitive evolution". It has been discussed in section 2.2.d. that support for the ecological hypotheses was indirect at best and had to be revaluated. This part focuses more particularly on the literature on the social intelligence/social brain hypothesis.

Maclean et al. precise that "the social intelligence hypothesis proposes that increased social complexity (frequently indexed by social group size) was the major selective pressure in primate cognitive evolution. This hypothesis is supported by studies showing a positive correlation between a species typical group size and the neocortex ratio, cognitive differences between closely related species with different group sizes, and evidence for cognitive convergence between highly social species" (original citations removed). Thus, the authors suggest that the social intelligence hypothesis is supported both by the correlation between a measure of social complexity and neocortex ratio, and by cognitive differences between closely related species. The literature they cite as a support for the second claim shows that primate (Maclean, Merritt, and Brannon 2008, Maclean et al. 2013, Sandel, Maclean, and Hare 2011) and bird (Bond, Kamil, and Balda 2003) species with rather similar brain size differ in some cognitive abilities suspected to be at play in social intelligence. Because brain size is highly correlated with neocortex ratio in anthropoid primates (figure 4.a.),

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the second claim thus appears to be in opposition with the first one.

The first claim, namely that brain size supports the cognitive abilities needed to deal with increasingly complex social environment is at the core of the social brain hypothesis ("the balance of evidence now clearly favors the suggestion that it was the computational demands of living in large, complex societies that selected for large brains", Dunbar and Shultz 2007a). As discussed in the first section, group size is not an optimal measure of social complexity. However, it has been suggested that other measures of social complexity were also related to brain size, supporting the social brain hypothesis. Dunbar and Shultz 2007a, in particular, noted that "a series of studies demonstrated that, among primates at least, relative brain size [usually indexed as relative size of the neocortex, the area that has disproportionately expanded in primates] correlates with many indices of social complexity, including social group size [...], number of females in the group, grooming clique size, the frequency of coalitions, male mating strategies, the prevalence of social play, the frequency of tactical deception, and the frequency of social learning" (original citations removed). There are several issues with the literature that Dunbar and Shultz 2007a used as a support for the social brain hypothesis. For example, Lindenfors 2005 used residuals from a regression of neocortex size onto total brain size and Dunbar and Shultz 2007b used neocortex residuals against rest of brain. These variables are only poorly correlated to neocortex ratio (figure 4.b.c.) and thus to absolute brain size. Note that the fact that these two variables are correlated is due to the structure of the data (in particular the high degree of correlation between brain size and neocortex size). These two variables do not have the same adaptative signification (using residuals removes most of the size effect). Also, Byrne and Corp 2004 argue that the use of deception in primate is linked to the absolute size of the neocortex, but not by the size of the rest of the brain, despite the very high correlation between the two (figure 4.d.). The reason is probably that the authors examined the effect of the size of the rest of the brain only after taking into account the size of the neocortex: thus they also removed the size factor of the rest of the brain. Finally most of these studies examined the neocortex ratio (Reader and Laland 2002 used the executive brain ratio which is closely related, see above), as if it was the most appropriate variable. Yet, the very idea that the neocortex ratio is the variable determining cognitive capacities is overly simplistic (see discussion in section 4). This can be understood by considering a hypothetical, tiny primate brain that would have a very large proportion of neocortex. Such a brain would probably be limited in term of processing capacities, despite having a large proportion of neocortex. The reason why neocortex ratio was adopted in this literature is that it was the measure that correlated the most with group size in primates (Dunbar 1992), and because "this index controls for changes in absolute size in a way that is independent of body size" (Pawowski, Lowen, and Dunbar 1998). As seen above, the idea that allometry had to be removed in order to obtain a variable that is adaptively meaningful is false on many grounds. In fact, due to the concerted evolution of brain structure within taxon cerebrotypes, the neocortex ratio is so closely related to absolute brain size (figure 4.a.) that two of the studies cited by Dunbar and Shultz 2007a actually estimated the neocortex ratio using the absolute brain size of the species (Kudo and Dunbar 2001, Pawowski, Lowen, and Dunbar 1998).

The above does not mean that the idea behind the social brain/intelligence hypothesis is false, but that it rests on weaker empirical and theoretical grounds than commonly assumed. This situation is not limited to the social brain/intelligence hypothesis. For example, Maclean et al. note that "both the percentage of fruit in the diet and social group size correlate positively with neocortex ratio in anthropoid primates", citing Barton 1996 and Dunbar and Shultz 2007b as support for their claim. Yet, Barton 1996 did not use the neocortex ratio, but the residuals of a regression of the independent contrasts in neocortex size onto the independent contrasts in the size of the rest of the brain. This variable is not equal to the neocortex ratio (see also figure 4.c.). Finally, the low level of resolution in most studies leads to confusing results. Maclean et al. for example note that social group size "covaries with the neocortex ratio in anthropoid primates" but that it is "unrelated to variance in self-control". Yet, these three variables are supposed to correlate with absolute brain size in primates (social group size: Dunbar 1992, neocortex ratio: Aiello and Dunbar 1993 (figure 4.a.), and self-control: Maclean et al.).

To conclude, the loose use of terms highlighted above as well as the lack of understanding of the methods used (for example, Reader and Laland 2002 noted that: "the disparities between brain measures suggest that either the three measures gauge different things, or some measures are more susceptible to type I or type II errors", italics added) has lead to a problematic situation where apparently contradictory results cohabit (e.g. "researchers have found that aspects of cognition [] positively correlate with absolute and relative brain size (brain size scaled to body size)", Stevens 2014, italics added). The framework discussed here permits to remove some of the misconceptions, to clarify some of the approaches and to improve some of the methods.

3. In view of the increasing sophistication of these techniques (Maclean et al. 2012), the use of phylogenetic methods has become the standard for comparative biology. Undoubtedly, these methods represent a major step forward for comparative studies, when, for example, examining the rate of evolution of one or several characters, or estimating the ancestral value of a character. But de-

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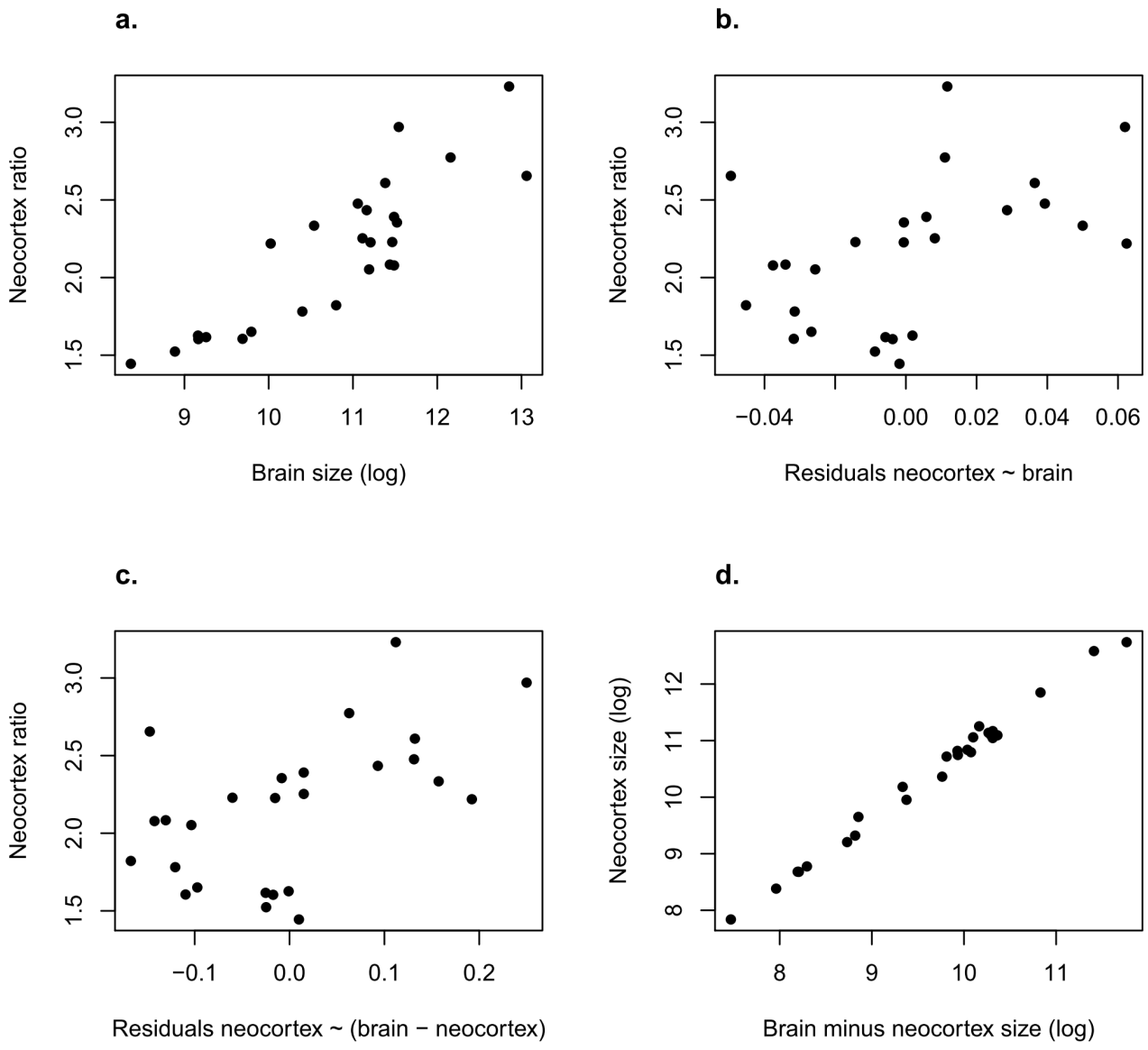

Figure 4: *Relationships between brain measures used in the literature of social brain/intelligence hypothesis. a. Relationship between neocortex ratio (obtained by dividing the size of the neocortex by the size of the rest of the brain) and brain size (Pearson correlation test: $t = 8.5649$, $df = 24$, p-value <0.001, $cor = 0.868$). b. Relationship between neocortex ratio and the residuals from a regression of neocortex size onto brain size (Pearson correlation test: $t = 2.5498$, $df = 24$, p-value $= 0.01759$, $cor = 0.462$). c. Relationship between neocortex ratio and the residuals from a regression of neocortex size onto the size of the rest of the brain (Pearson correlation test: $t = 3.1551$, $df = 24$, p-value $= 0.004281$, $cor = 0.541$). d. Relationship between the size of the neocortex and the size of the rest of the brain (Pearson correlation test: $t = 53.7856$, $df = 24$, p-value <0.001, $cor = 0.996$). Data from Stephan, Frahm, and Baron 1981.*

spite the global embracement for this kind of method, there are several points that must be noted, particularly concerning the techniques used for analyzing the relationship between variables (e.g. phylogenetic generalized least-squared model). These methods, used here by Maclean et al., are designed to take into account the lack of independency of the data points due to the phylogenetic relationships between species. First, phylogenetic methods have assumptions on their own that must be properly assessed (including in the construction of phylogenetic trees; see Pozzi, Bergey, and Burrell 2014). Second, phylogenetic methods do not overcome the problem arising from a problematic sample of species (mixing taxon-cerebrotypes and/or selective sampling of species inside a taxon-cerebrotype). Consider for example, that such techniques are used to remove the effect of potential

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grade shifts; that are defined as "a shift in the relationship between the main variables with no change in their slopes" (Nunn and Barton 2001). Grade shifts indicates that the relative value of the two variables tested differs between the two groups, and so probably is the value of the other variables influencing or being influenced by the variables of interest. Statistically removing the effects of grade shifts using phylogenetic methods is therefore equivalent to comparing variables not necessarily comparable. Inversely, therefore, the lesser such a sampling problem affects an analysis, the lesser impact the phylogenetic methods are likely to have on the estimation of the parameters. Moreover, the potential gain in precision obtained by using phylogenetic methods is partly counter-balanced by the fact that phylogenetic analyses often render part of the biological interpretation harder to make. The use of phylogenetic methods must therefore be properly evaluated.

4. Similar experiments done on a large number of species is the only way for comparative psychology to obtaining reliable results. As such, Maclean et al.s study is an important step forward in comparative psychology, as it opens the door to a promising new era where the power of the comparative approach will be fully exploited (see also Maclean et al. 2012). However, this pioneering study took a very long time to be completed (about seven years). Therefore, considerable effort should be dedicated to render such kind of study much more easily feasible, in particular by increasing the number of laboratories involved and the efficiency of the collaboration.

Moreover, there are a few points that need to be addressed by future studies. In particular, the entire data from all subjects should be systematically given. In addition, it is important to escape the yes/no approach and test, for example, the number of trials needed before the individual learns the correct answer or the distribution of correct answers for each animal (see also Wright 2013). In Maclean et al. analysis, this would mean the individual and trial data during the habituation to the task (or during the first two presentations for the A-not-B test) and during the test (for the transparent cylinder test). The large inter-individual differences inside a species (for example in squirrels) should also encourage testing for the effect of personality on these results. Another interesting aspect to add to the analysis is proposed by Auersperg, Gajdon, and Bayern 2012; who suggest considering how species and individuals approach different tasks. Another potentially useful data would be, if relevant, the place of the individual in the social group. There is also no alternative for comparative psychologists and neuroscientists (see also Striedter et al. 2014) to construct a very large, open access database on brain and behavioural measurements.

IV. A synthesis on comparative studies of brain and behaviour

A. The evolutionary approach

Maclean et al. note that their results "suggest that increases in absolute brain size provided the biological foundation for evolutionary increases in self-control". Notwithstanding the comments above, the authors thus assume that comparative analyses allow a better understanding of the mechanisms underlying a behavioural capacity. This issue has been addressed by a series of recent papers. In this sub-section, Bolhuis and Wynne 2009 opinion article "Can evolution explain how minds work?" published in the journal Nature is critically reviewed in order to address some of the conceptual and methodological difficulties of this question.

Firstly, since the authors repeatedly refer to Darwin, and although it does not affect the rest of their paper, it is important to note that Darwins claim that there is "no fundamental difference between man and the higher mammals in their mental faculties" is not built "on the basis of his belief that all living species were descended from a common ancestor", as Bolhuis and Wynne note, but on his evaluation that many mental faculties found in humans were also found in some non-human animals. Secondly, after discussing the fact that in many cases, demonstrations in non-human animals of faculties that we know exist in humans have flaws in their design that affect the validity of their conclusions, Bolhuis and Wynne state that: "such findings have cast doubt on the straightforward application of Darwinism to cognition". Yet the demonstration that some previous experiments suffered from methodological issues does not give, a priori, more legitimacy to alternative hypotheses. Scientific rigor requires that the value of a hypothesis must be evaluated in regards to the weight of the evidence only ("evidentialism", e.g. Fitzpatrick 2008); and not on its (subjective) simplicity.

Moreover, Bolhuis and Wynne repeat a widespread misconception that finding functional gaps between human cognitive abilities and that of other species would prove Darwin's idea about continuity of mind (in particular his claim that "the difference in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind", Darwin 1871, p.105) to be false (see also Penn, Holyoak, and Povinelli 2008). This claim is based on a biased interpretation of Darwin's idea. First, Darwin made it clear that his use of the word "mind" was not restricted to "cognition" (that he sometimes refers to as "intellect"), but instead included "senses and intuitions, the various emotions and faculties, such as love, memory, attention, curiosity, imitation, reason, &c." (p.105). Thus, finding some func-

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tional differences between some of these abilities does not necessarily falsify the claim as a whole. Second, Darwin was aware that evolution created "breaks", including between humans and other species' minds. For example, he considered that "the moral sense perhaps affords the best and highest distinction between man and the lower animals" (p.106, italics added to highlight one true mistake) and he listed a number of characteristics that he believed were functional gaps between humans and apes (tool construction, metaphysical and mathematical reasoning, language, and a "disinterested love for all living creature", p.104-105).

In the second paragraph of their paper, Bolhuis and Wynne give two examples showing that "cognitive traits cannot be neatly arranged on an evolutionary scale of relatedness". And in a latter paper, Hemelrijk and Bolhuis 2011 referred to these examples with the following line: "given that evolutionary relatedness is not a good predictor of the occurrence of vocal imitation in different taxa, and completely inadequate when it comes to language, Bolhuis and Wynne concluded that evolution cannot explain how minds work". Although this claim is analyzed in more details below, it is clear that the strong version of this claim is not true. As discussed above, Bolhuis and Wynne reduce the concept of "mind" to the one, much narrower, of "cognition". The mind represents the whole set of mental operation in a species. It includes the sensory-motor system, emotions, attention, cognition and, perhaps above all, consciousness. The organ responsible for the mind is the brain. The brain is not a homogeneous structure and some of its features have appeared at different periods during animal evolution. The way these features have evolved makes possible some neural process and renders impossible others. As such, evolution does permit to understand some aspects of the mechanisms underlying the animal mind.

Bolhuis and Wynne further note that: "the difficulty of not knowing whether shared ancestry or convergence accounts for similar cognitive outcomes in different species is not the only problem with applying an evolutionary approach to cognition". It is unclear why this is a problem at all. In fact, one of the main issues with Bolhuis and Wynne's account is that the authors believe that "evolutionary analyses [...] are analyses of history". Evolution is a process based on variation, heredity and selection of characters; leading to a diversity of life forms. Therefore, evolutionary analyses are not just analyses of the presence of a character over evolutionary time (its history), but also studies of the occurrence of the character in relation to other characters and the environment (its selection). The fact that apparently "similar cognitive outcomes" can come from very different brains is one of the reasons why comparative analyses should compare comparable species and not a priori extend conclusions from one taxon to another, as noted above. But homoplasies are not a problem for comparative studies. Instead, they represent different opportunities to understand the evolution of a feature.

In regards to the present paper, one of the most important aspects of Bolhuis and Wynne's paper is that the authors minimize the possible impact of a neuroecological approach by critically analyzing the supposed relationship between food-storing capacities and hippocampal enlargement in birds. However, both the original research and the critics by Bolhuis and Wynne suffer from a number of problems. Indeed, the neuroecological approach is based on a three pillars strategy, namely (1) a detailed knowledge of species differences in brain anatomy and physiology, and (2) on species differences in behaviour and (3) an understanding of the scaling methods of brain features. None of these pillars were sufficiently present in previous literature on neuroecology. Data on brain anatomy was often at low resolution and from different sources (Roth II et al. 2010). Moreover, the behaviours studied were often not reduced to their simplest forms. For example food caching behaviour varies in the duration of remembrance and can range from learning a set of simple rules of caching to managing multi-dimensional maps in which the position, content, time of deposit and even potential thieves present at that time are remembered (see for example Clayton, Dally, and Emery 2007), and these differences have not been systematically considered in the literature. Finally, there was also, as discussed above and below, no real theoretical understanding of the differences between scaling methods ("in the absence of theoretical principles, progress will be made when investigators compare a variety of scaling methods with regard to their ability to predict independently derived behavioural indicators of cognition", Deaner, Nunn, and van Schaik 2000). With the development of these three pillars, the neuroecological approach could greatly improve our understanding of brain and behaviour (Smulders, Gould, and Leaver 2010).

Still, Bolhuis and Wynne argue that results from evolutionary analyses "would have to be verified using controlled experiments" because, they argue, "questions about the causal underpinnings of behavioural differences can be elucidated only with a causal analysis". Bolhuis and Wynne thus extend their claim about using a causal analysis to understand the mechanism of behaviour to now understand the mechanism of "behavioural differences" between species. These are not identical claims. With a causal analysis, it is theoretically possible to study and understand the mechanisms underlying behaviours such as song production. It is possible to know, for example, that for such and such behaviours, such and such structures are working and to know how they are working, that affecting one structure affects a number of known behaviours, or that removing another structure prevents for other behaviours, etc. But consider the hypothetical case where it is possible to

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control every features of every particular structure in the bird brain, and that such knowledge is used to apply a causal analysis aimed at understanding the "causal underpinnings of behavioural differences" in song repertoire size. As such every feature of the bird brain is carefully tested, trying to find individuals with larger repertoire size. However, even with the right set of features modified, it is unsure that these birds will sing a larger repertoire, because the proper ecological, social and motivational conditions for them to learn and/or sing may be absent. In these cases, evolutionary analyses can come up with elements of responses (see below).

Therefore, evolutionary analyses have the potential to improve the understanding of the mechanisms of psychology. Although inter and intra species levels cannot be directly compared (Willemet 2013), results from one level can be used to study the other. Moreover an interesting, intermediate level is the population level (e.g. Pravosudov and Clayton 2002). Other levels of particular interests are comparisons between domestic/wild/feral forms as well as different breeds of domestic species (Willemet 2013). These levels of analyses are probably the most serious chances for rapidly improving our understanding of the evolution of brain, cognition and behaviour. It is therefore particularly problematic that most research effort has concentrated on the study of taxa that present much more complex patterns and are therefore much less able to increase our knowledge on the evolution on brain and behaviour (the extreme of this trend being comparisons between human and chimpanzee brains, see Willemet, in prep.).

The comparative approach is fundamentally limited, however, because many aspects of brain and behaviour evolution may not be easily discernable for the human observer. It is also limited because, as noted by Striedter 2005, "not all evolutionary changes have occurred more than once". Yet, while Bolhuis and Wynne seem to defend a view where causal analyses are sufficient, it is interesting to note that understanding the neural bases of behaviour in the nematode *Caenorhabditis elegans* is proven exceedingly difficult, even though researchers working on this species use a degree of sophistication of methods and data far beyond anything applied to the two most studied taxa; birds and mammals. Moreover, because several orders of magnitudes separate the complexity of *C. elegans*'s nervous system and behaviours compared to those found in birds or mammals, the role of evolutionary studies and the hypotheses they can produce in understanding the mechanisms of cognition and behaviour is likely to be significant. It should also be noted that, providing that a large dataset is assembled in the first place, and given the methods currently available, the neuroecological approach is far less destructive in generating and testing hypotheses on these mechanisms. Good science admits no such thing as "naïve evolutionary presuppositions" (Bolhuis and Wynne 2009), but it welcomes evolutionary insight.

B. Comparative approach: variables

A precise account of the brain mechanisms underlying animal behaviour will need to include detailed descriptions at a fine level of detail (such as the number, composition and nature of the cells, the connections, the neurotransmitters/neuromodulators involved). But with such a level still out of reach, researchers can focus on larger levels. Brain size, as seen above, only has a limited utility. However, brain composition in term of structure size is likely to be significant when it comes to species behavioural differences. But how to measure this effect inside a taxon-cerebrotype? The discussion above provides a draft of such a theoretical framework that would ultimately permit to better understand the variables that are at play in explaining species differences in behaviour.

B.1 Absolute structure size

With a larger number of neurons and connections, a larger structure is theoretically endowed with more processing capacity than a smaller one (Striedter 2005). In an ideal case where a brain structure is dedicated to a unique function that can be measured, species absolute abilities for this function should be directly related to the size of this brain structure (or more precisely, its number of cells and connections), irrespective of the size of the other structures. However, one structure is rarely responsible for a single ability, and in most cases species also differ in the size of other brain structures. As discussed above, as the other structures are selected and get more neurons, a structure, even without direct selection on its processing capabilities, may need to increase its number of neurons only for its neuronal output not to be too much diluted in such a larger brain structure network. This adjustment effect might be variable from one structure to another (in particular, relatively small structures might be more affected by it than larger structures, although some very small structures might appear almost unaffected if they coevolved with other structures amplifying their output (this may be one explanation for the weak increase in size despite extreme variation in brain size in some structures such as the suprachiasmatic nucleus (Pinato et al. 2007))), although the factors implied are yet to be determined.

B.2 Proportional structure size

Because a relatively larger structure may be able to connect more extensively with other structures than a smaller one (Striedter 2005), a correlation between the proportional size of a structure and its influence on the brain network is to be expected. However, no direct relationship is likely to exist. Indeed, small variations in the proportional size of smaller structures are likely to

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be more significant than for larger structures, because they necessitate relatively larger differences in their absolute size (Willemet 2013). Moreover, the proportional size of a structure is unlikely to be the factor underlying a structures processing capacity because it does not take the absolute size of the structure into account, that is, the number of neurons.

B.3 Relative structure size

Most studies to date, in particular those looking at the neurological correlates of caching behaviour, have analysed the relative size of a structure, defined as the residuals of a structure onto the size of the brain (or the telencephalon in some studies). The necessary assumption behind this method is that two structures of different sizes would have the same processing capabilities as long as their relative (residual) size in the brain are similar. In other words, this approach assumes that size residuals would have the same absolute advantage in term of the function considered. In the framework of brain evolution discussed above, such assumption is only plausible in the taxon cerebrotypes where the absolute size of a structure is not or only weakly related to its processing capacity dedicated to the function of interest, or in the taxon-cerebrotypes where the absolute size of a brain structure correlates with its relative size in the brain (see sub-section 4.C.).

B.4 Proportional and relative structure size compared to another structure or a group of other structures

The two preceding methods involve taking into account the size of the brain, that is, the size of all the structures. This is potentially useful, as discussed above, because it enables to evaluate the size of the entire brain network, and therefore the potential fraction of the size of a structure that must adjust with the increasing number of neurons in the other structures. As such, however, these methods are subject to the part-whole problem. That is, the size of the structure of interest is included in the brain size variable used in the analysis. The extent to which this factor influences the analyses is related to the size of the structure considered. An analysis regressing the size of the neocortex onto the size of the brain will be highly affected, as the size of the neocortex represents the main fraction of brain size. An analysis focusing on a smaller structure should be less affected by the part-whole problem, but the situation would not be better. Indeed, small variations in the size of the larger brain structures can hide significant variations from smaller structures. One solution for these problems is to use the size of the brain minus the size of the structure of interest. Here, too, there will be an effect that depends on the size of the structure. Removing a large structure will have a large impact, whereas the impact will be smaller for a small structure.

Therefore, instead of taking the size of all the other structures into account, it is possible to take one structure or a group of structure in particular as a reference. The outcome of such an analysis will depend on a number of factors. The proportional size of a structure in a group of structure can vary with the cumulated size of the group of structure (as seen in the concerted evolution of brain structures inside a mammalian taxon cerebrotype for example, see Willemet 2012). This does not necessarily mean that the relative influence of each of the structure of the system varies too. It may be that each structure has a distinct connectivity pattern, with some structures needing more spacing, and/or, larger number of neurons, when increasing their processing abilities to a factor equivalent to other structures. For example, increasing the processing capacity of the primary visual cortex by a factor two may need more neurons and less axon length compared to increasing the processing capacity of the prefrontal cortex by a factor two. In that case, the proportional size of the structure inside the system will not be an indicator of the structure relative importance in the system of structure. Because in that particular case it is related to the absolute size of the structure, however it could be an indicator of the structure absolute processing capacity. However, here again the size of the structure or its number or neurons cannot be easily compared (10 grams of cerebellum may be able to do more operations than 10 grams of frontal cortex, but these operations may not be directly comparable). Passingham and Smaers 2014 assumed a direct link between the proportional size of a structure and its processing capacity. However, there can be no direct relationship between these two variables because the proportional size of a structure does not directly take into account the absolute size of the structure. What about the relative size of these structures compared to the size of the other structures? Residuals of the size of a structure onto the size of the other structures will be evidence of particular selection on this structure. However, it will not necessarily be an indicator of the structure absolute functional capacity, unless most of the increase in size in the whole system of structure is uncorrelated with their functional capacity. The relative size of a structure is unlikely to capture most of the characteristics of the structure underlying species differences in the ability supported by the structure. This is because residuals remove most of the size factor of the structure. The combination of these systems leads to complex situations. For example, the neocortex has generally increased in size disproportionally compared to the other structures in primates, betraying selection on this structure. At the cellular level, the ratio of number of neurons in the cerebellum and neocortex remains almost constant (Herculano-Houzel 2010 see also Barton and Venditti 2014). This does not mean that the selection for these two structures has been of

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similar importance (since they have different patterns of connectivity), nor that these two structures have a comparable influence in the brain network.

The main difficulty for comparative studies of brain and psychology is that it will often be a combined effect between all the factors described above. And thus none of the individual methods is likely to tell the whole story. On the other side, analyzing the relative influence of each of these methods makes it possible to better understand the factors influencing the relationship between a structure and its functional and processing capacities. Potential difficulties and preliminary conclusions when using these methods are illustrated below.

C. Case analysis: neural correlates of song repertoire in birds

Moore et al. 2011 conducted an ambitious analysis of the neural correlates of species differences in song repertoire. The authors have assembled a large dataset comprising measurements of 1 to 3 variables (volume, neuron number, neuron density) for various brain nuclei in 49 species of songbirds. Before analysing some of the conclusions of Moore et al. 2011, it is necessary to note, as the authors did, that repertoire size is not the ideal variable because it is only one of the characteristics of song behaviour, and there is no strict correspondence between repertoire size and any single brain nucleus. Also, the authors mix different families of passerines, even though substantial differences in brain anatomy may exist between these families (there might be several taxon-cerebrotypes that would be better individually examined). However, a quick examination of the data reveals no obvious differences between the families (figures 5 and 6). This suggests that the different families can be studied together.

The present discussion focuses more particularly on one of the conclusions of Moore et al. 2011, namely that "the size of upstream areas relative to their downstream targets can be a superior indicator of behavioral abilities than the relative size of an entire neural pathway" (Moore et al. 2011). This claim refers to various elements that can be examined in regards to the framework discussed above. First, the authors focus on the size of the song system relative to the size of the brain. This is not a trivial choice, since, as discussed above, the absolute size of a structure (or a system) matters when it comes to processing power. Here, it is interesting to understand why the relative size of the song system appears to be linked to the song repertoire variable (figure 7.a.). Could a small system in a small brain do better than a larger system in a larger brain? As suggested by the discussion above, this is possible if the absolute size of a structure mainly supports factors others than functional capacity. Here it is apparently not the case, as the absolute size of the song motor pathway correlates with repertoire size (figure 7.b.). The contradiction is only apparent, because those species that have a relatively larger song system also have an absolutely larger song system (figure 7.c.).

Focusing on two nuclei of the song motor pathway; HVC and RA (robust nucleus of the arcopallium), for sake of simplicity, the framework above allows the examination of the effects of proportional, relative and absolute size of the brain nuclei on song repertoire. In order to fully understand the situation, it is first interesting to note that the absolute, relative (residuals from a regression onto RA size) and proportional (divided by RA size) size of HVC correlate with each other and with song repertoire (figure 8). Note that using neuron number instead of volume does not affect the relationship described above due to the high correlation between these two variables in HVC and RA (figure 9).

A strong interpretation of the hypothesis proposed by Moore et al. 2011, i.e. that the relative size between structures of a system matters more than their absolute size is complex to interpret in view of the framework discussed above. A critical test of this claim can be done by considering two species with a similar size of HVC but with different sizes of RA. The data suggests that for similar HVC size, the species having the smallest RA (and therefore the highest ratio) have a larger song repertoire than the species with the largest RA (figure 10.a.). How could a small RA do better than a larger one? The key is that the pattern seen in figure 10.a. probably needs to be interpreted the other way around. That is, instead of species with similar HVC size and small RA having larger song repertoire than species with larger RA; the correct interpretation seems to be that species with larger song repertoire have enlarged their HVC compared to their RA (figure 10.b.). This is supported by the fact that the relative size of HVC compared to RA is correlated with the relative size of HVC onto the telencephalon, and in the brain minus telencephalon (figure 11). Moreover, the relative size of HVC onto RA and of RA onto nXIIts (the tracheosyringeal portion of the hypoglossal nucleus) correlates with HVC and RA, respectively (figure 12). As such, this is entirely compatible with the framework developed above.

The other intriguing question is why would RA enlarge if not needed as much as HVC? There are two elements of response. The first is that RA enlargement could be a necessary feature of an otherwise enlarged telencephalon, due to the adjustment effect discussed earlier in the text (figure 13). The second could be purely adaptative. Although rather low, there is a correlation between the size of RA and song repertoire (figure 14), so that larger RA can ultimately be needed to process larger song repertoire.

Moore et al. 2011 focus on the concepts of "encephalization" and "neocorticalization", defined as "wherein behaviors are linked to the size of the whole brain relative to body size or the isocortex relative to the rest of the brain, respectively". However, both views are

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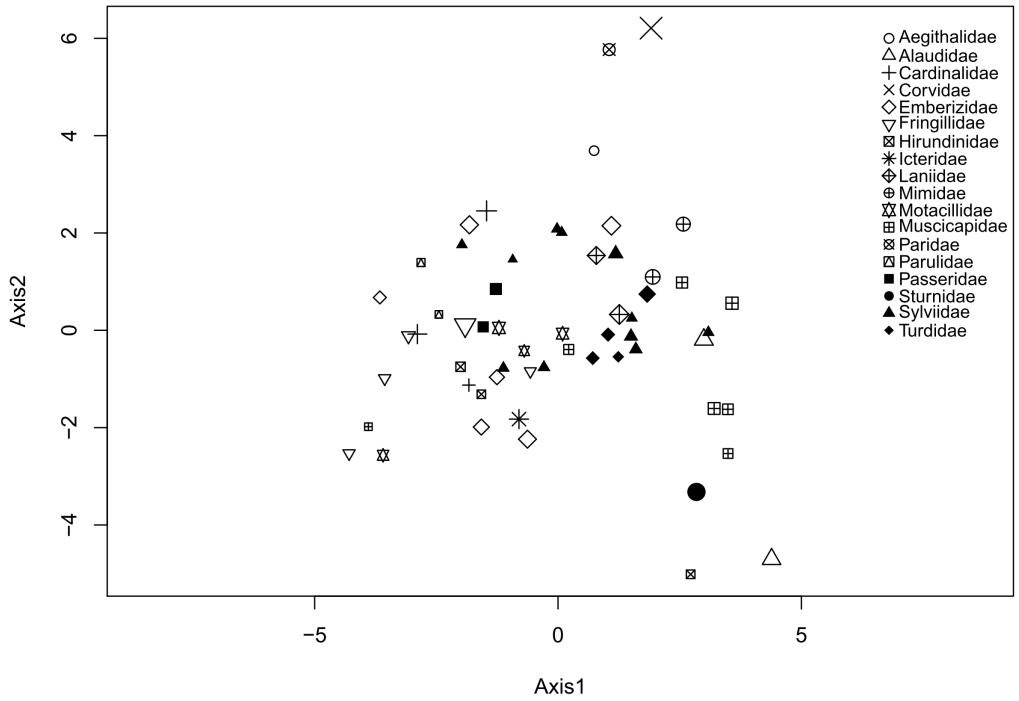

Figure 5: *Principal component analysis of the proportional size of the brain regions measured by Moore et al., 2011 (telencephalon and mesopallium excluded). Bird families cannot be easily separated on the basis of this analysis alone.*

problematic. The first one, which corresponds to relative encephalization in the terms defined earlier in the text, is necessarily limited for the reasons discussed in section 2.2. The second one is also limited, because, as discussed above, there can be no simple relationship between the relative size of a structure and its processing capacity. Moreover, the authors mix several concepts that make some of their analyses difficult to interpret. For example, they examine "whether syllable repertoire size related more strongly to the relative size of the entire song system (akin to encephalization) or to relative size differences between nuclei (neocorticalization)". By doing so, they equal the concept of relative encephalization (that they call encephalization) to the relative size of a neural system inside the brain, even though these two are very different concepts. Also, some of the variables used by Moore et al. seem unnecessary complex and participate in blurring the relationships between song repertoire and its neural basis. For example, the authors note that "HVC volume was strongly related to HVC# (r = 0.98, P <1.0 10 16) but not to neuron density (P = 0.44) after controlling for BSS" (Moore et al., 2011, where # symbolises neuron number, and BSS the size of the brain minus the size of the song system). Yet, because the size of the song system is small (usually less than one percent of the total brain volume), the value BSS is almost equal to the size of the brain. Moreover, why controlling for the size of the brain, or, in other words, why focusing on the relative size of a brain structure? As discussed above, there is no reason why the relative size of a structure should be the a priori level of interest. In fact, both neuron number and neuron density are correlated with absolute HVC volume (figure 15).

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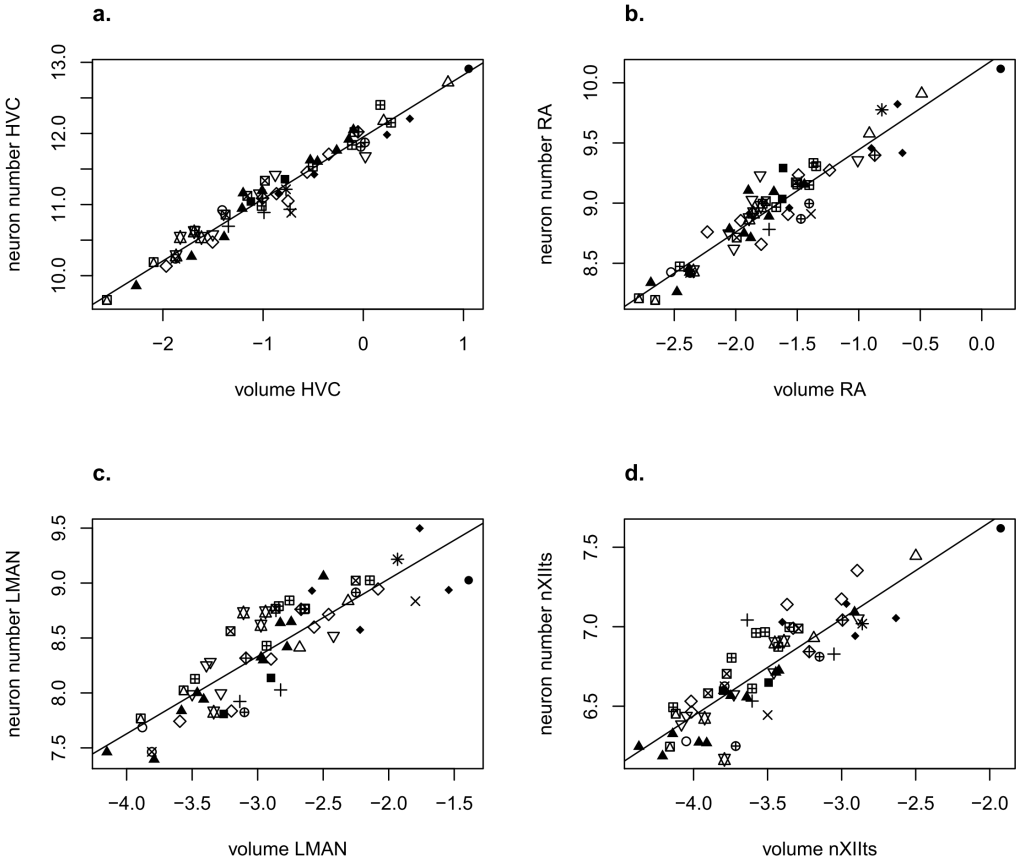

Figure 6: *Size of the song nuclei onto their number of neurons. Symbols for families are similar to figure 5. There are no obvious differences between families.*

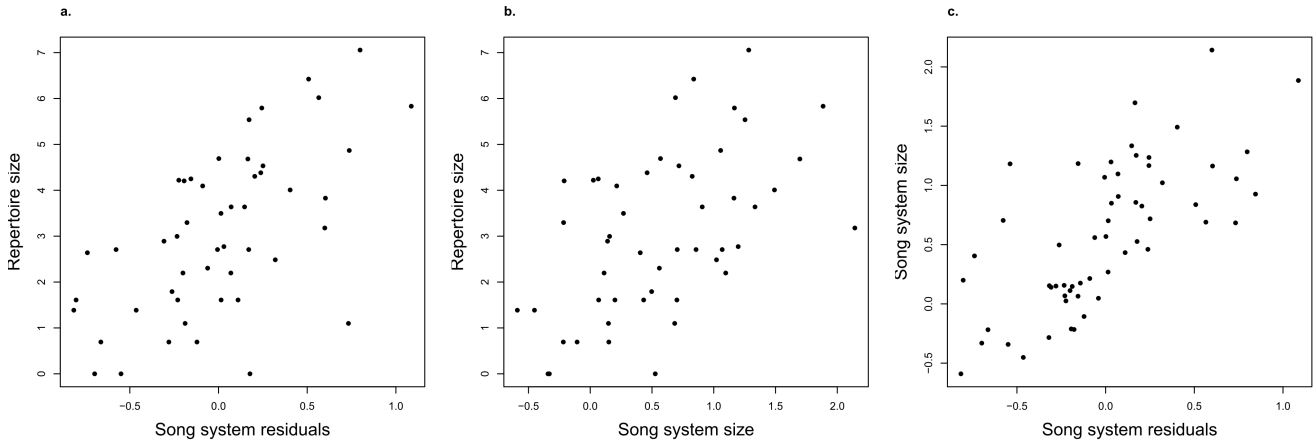

Figure 7: *Relationships between song repertoire size, song system size and song system residuals (obtained after linear regression onto brain size (log)). a. Pearson correlation test between repertoire size (log) and song system residuals: $t = 5.2628$, $df = 47$, p-value < 0.001, $cor = 0.61$; b. Pearson correlation test between repertoire size (log) and song system size (log): $t = 4.3769$, $df = 47$, p-value < 0.001, $cor = 0.54$; c. Pearson correlation test between song system size (log) and song system residuals: $t = 7.2139$, $df = 56$, p-value < 0.001, $cor = 0.69$.*

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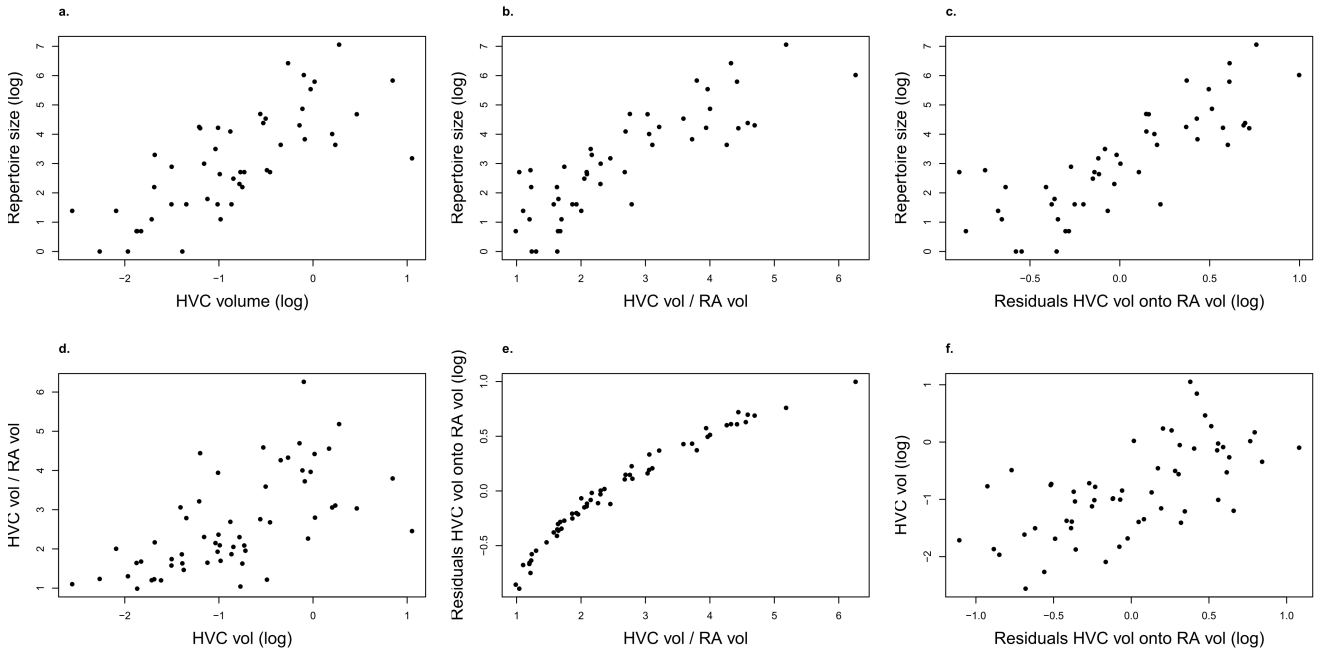

Figure 8: . *Relationships between song repertoire size and different measures of HVC size. a. Pearson correlation test between repertoire size (log) and absolute HVC volume: t = 7.6375, df = 47, p-value <0.001, cor = 0.74; b. Pearson correlation test between repertoire size (log) and proportional HVC volume: t = 10.9364, df = 47, p-value <0.001, cor = 0.85; c. Pearson correlation test between repertoire size (log) and relative HVC volume: t = 9.5065, df = 47, p-value <0.001, cor = 0.81; d. Pearson correlation test between proportional and absolute HVC volume: t = 6.1592, df = 56, p-value <0.001, cor = 0.64; e. Kendall correlation test between relative and proportional HVC size: z = 10.4846, p-value <0.001, tau = 0.95; f. Pearson correlation test between absolute and relative HVC size: t = 6.3635, df = 56, p-value <0.001, cor = 0.65.*

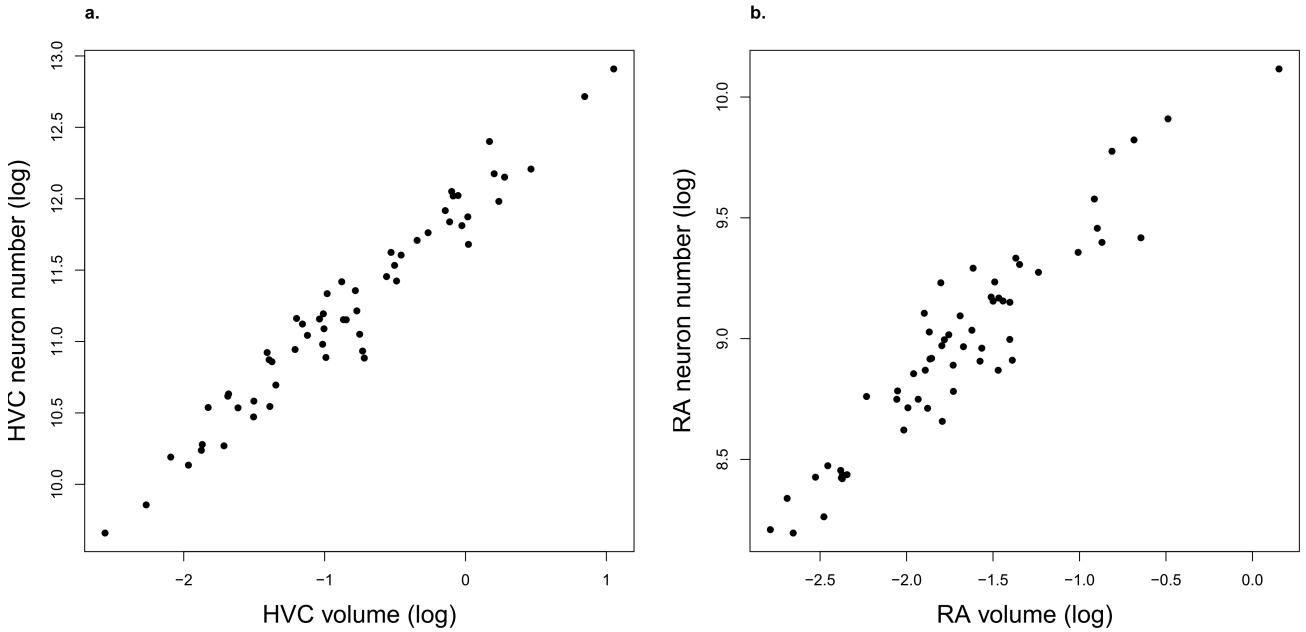

Figure 9: *Relationships between structure size and neuron number in HVC (a) and RA (b). a. Pearson correlation test: t = 33.1202, df = 56, p-value <0.001, cor = 0.98; Pearson correlation test: t = 22.3498, df = 56, p-value <0.001, cor = 0.95.*

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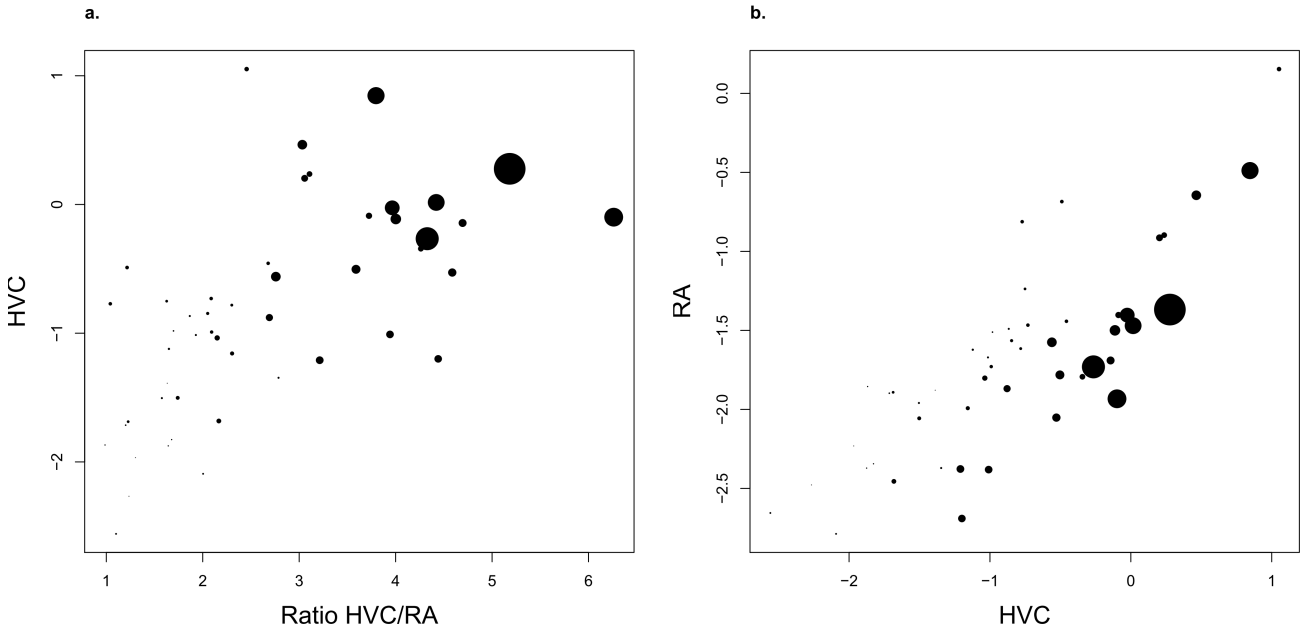

Figure 10: *a. Size of HVC onto the ratio between HVC and RA. b. Size of RA onto the size of HVC. The size of the symbols is proportional to the size of the song repertoire.*

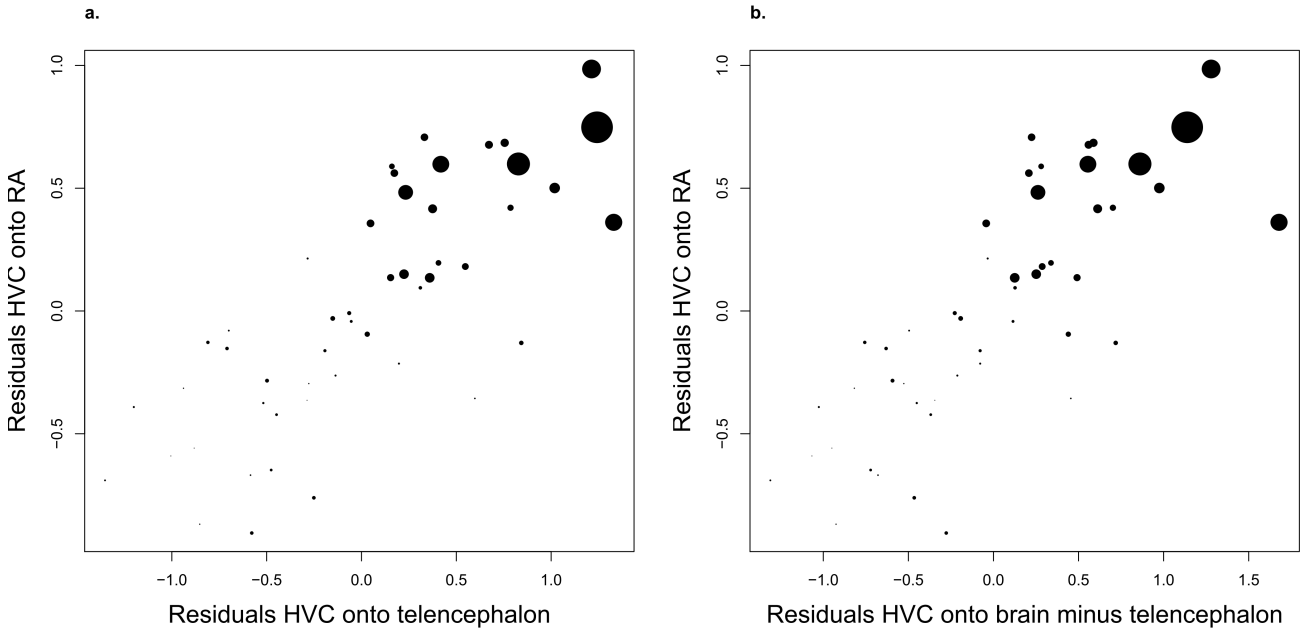

Figure 11: *Residuals of a linear regression of HVC onto RA volumes onto residuals of a linear regression of HVC onto a. the telencephalon (Pearson correlation test: $t = 8.4345$, $df = 47$, p-value <0.001, $cor = 0.78$), and b. the brain minus telencephalon (Pearson correlation test: $t = 8.8799$, $df = 47$, p-value <0.001, $cor = 0.79$). Volumes are logged. The size of the symbols is proportional to the size of the song repertoire.*

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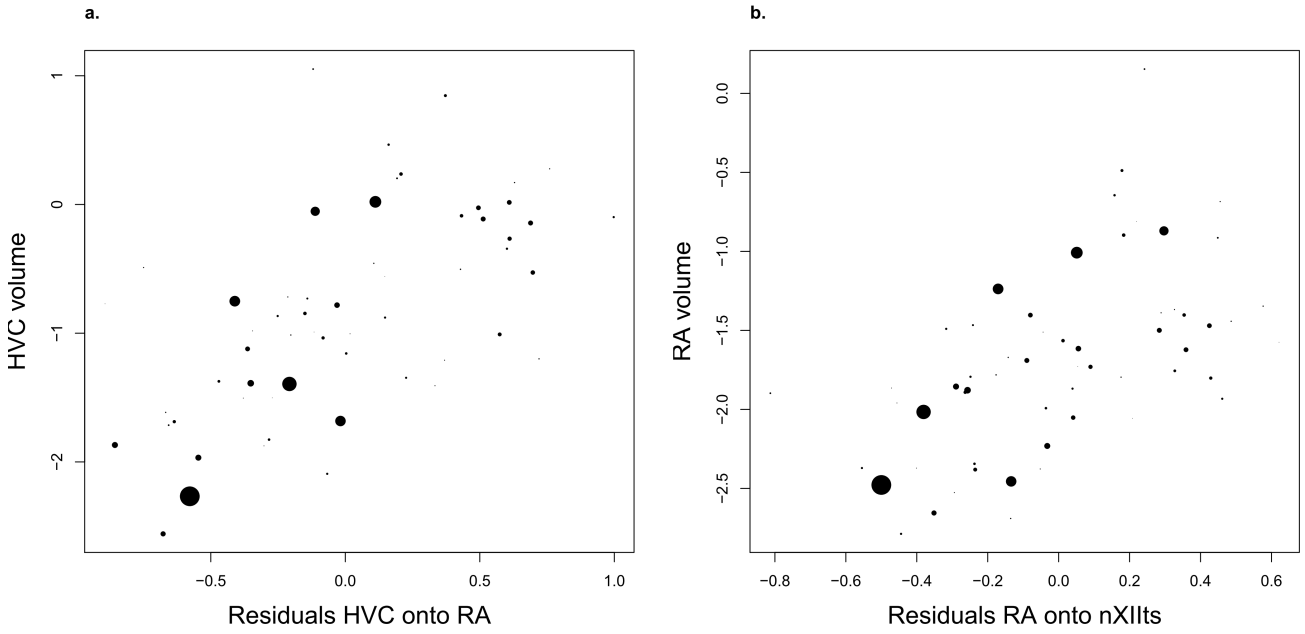

Figure 12: *The relative size of HVC onto RA and RA onto nXIIts correlates with HVC and RA, respectively. a. HVC onto RA. Pearson correlation test: t = 5.0216, df = 47, p-value <0.001, cor=0.59; b. RA onto nXIIts. Pearson correlation test: t = 4.2985, df = 47, p-value <0.001, cor= 0.53. The size of the symbols is proportional to the size of the song repertoire.*

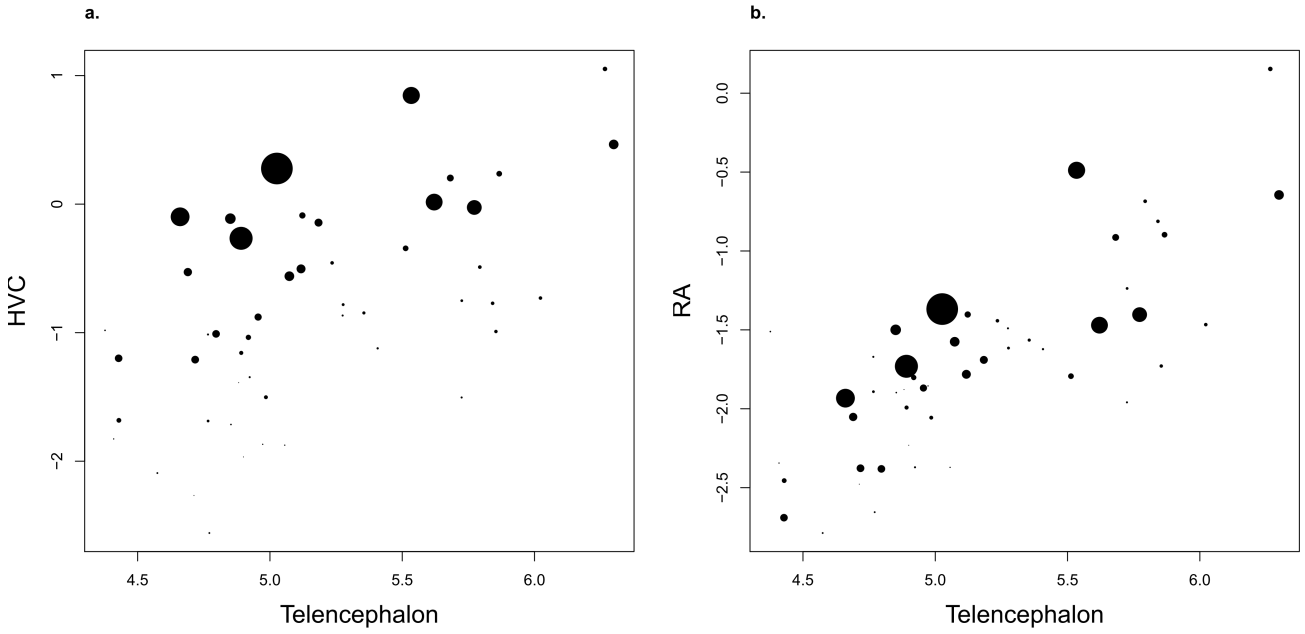

Figure 13: *a. HVC volume onto telencephalon volume (log); Pearson correlation test: t = 4.8796, df = 47, p-value <0.001, cor = 0.58. b. RA volume onto telencephalon volume (log); Pearson correlation test: t = 8.2988, df = 47, p-value <0.001, cor = 0.77. The size of the symbols is proportional to the size of the song repertoire.*

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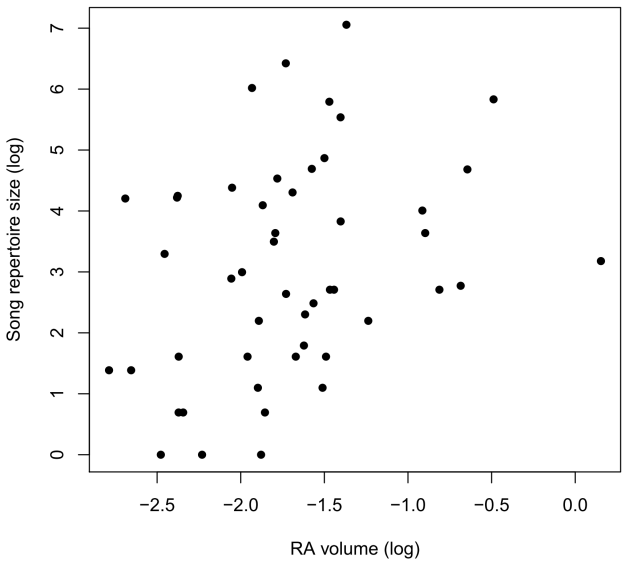

Figure 14: *Song repertoire size onto RA volume. Pearson correlation test: t = 2.3812, df = 47, p-value = 0.02136, cor = 0.33 (with the outlier common starling (Sturnus vulgaris) removed: t = 2.6399, df = 46, p-value = 0.01128, cor = 0.36).*

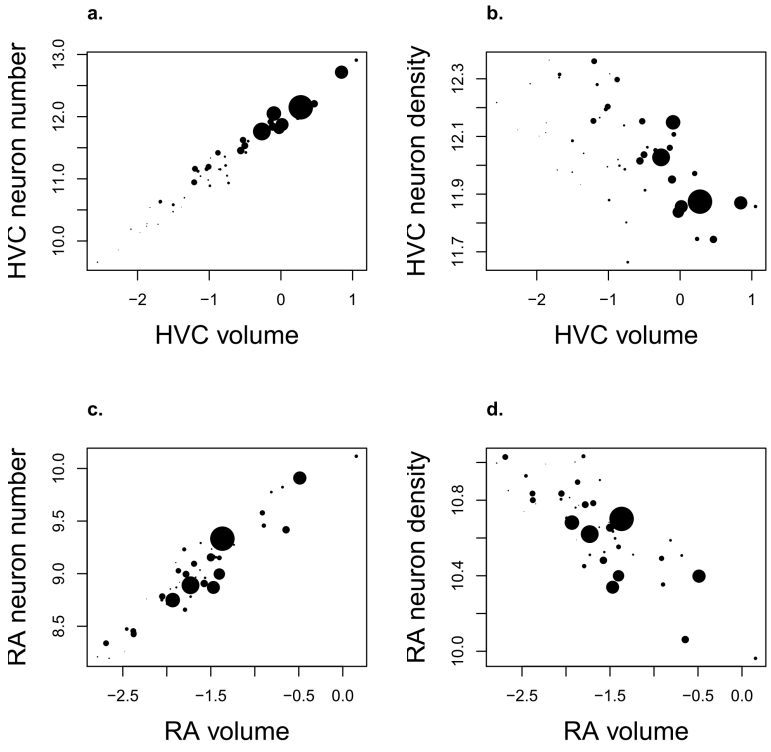

Figure 15: *a. HVC volume onto HVC neuron number. Pearson correlation test: t = 35.1313, df = 47, p-value <0.001, cor = 0.98. b. HVC volume onto HVC neuron density. Pearson correlation test: t = -4.9558, df = 47, p-value <0.001, cor = -0.59. The size of the symbols is proportional to the size of the song repertoire. c. RA volume onto RA neuron number. Pearson correlation test: t = 21.192, df = 47, p-value <0.001, cor= 0.95. d. RA volume onto RA neuron density. Pearson correlation test: t = -9.2068, df = 47, p-value <0.001, cor = -0.80. The size of the symbols is proportional to the size of the song repertoire.*

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In conclusion, the framework above could ultimately allow a better understanding of the functional significance of the size of brain structures. Moreover, although major lineages are lacking and the species represented represent only a fraction of the songbird species, the dataset assembled by Moore et al. (2011) has probably a lot to reveal. For example, with a few exceptions, there seems to be a correlation between the residuals of a linear regression of HVC onto RA and of Area X onto RA (figure 16). This suggests that at least some structures from the song motor pathway and the anterior forebrain pathway evolve within a system.

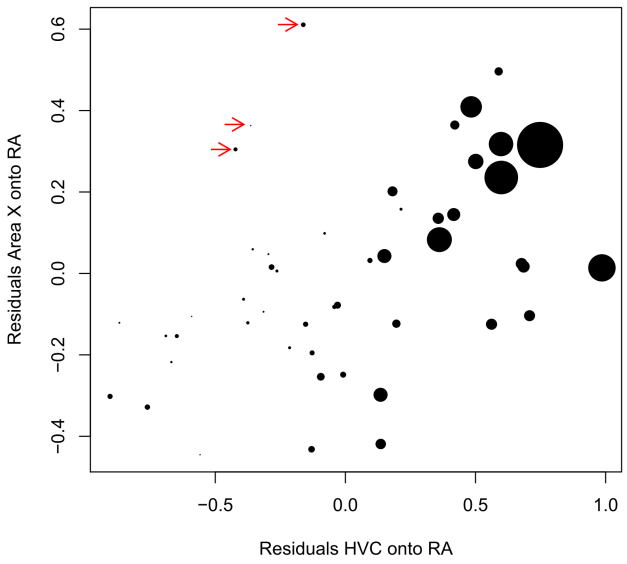

Figure 16: *Residuals of a linear regression of HVC onto RA onto residuals of a linear regression of Area X onto RA. Pearson correlation test: $t = 3.4021$, $df = 47$, p-value $= 0.001375$, $cor = 0.44$. With the three outliers excluded (red arrows: Catharus fuscescens, Locustella luscinioides, Emberiza calandra), Pearson correlation test: $t = 4.8679$, $df = 44$, p-value <0.001, $cor = 0.59$. The size of the symbols is proportional to the size of the song repertoire.*

Conclusion

The present paper and the previous one aimed at encouraging readers to engage in a constructive critic of the fields of comparative neuroscience and psychology, to reconsider some of the concepts and methods that most consider granted and to (re)discuss a new framework on the evolution of brain and behaviour. Although most of the issues discussed here need to be further studied, it should not be contentious to conclude the present paper by the following remark: studying a measure as imprecise as a composite measure of self-control obtained by averaging the results from two tests moderately correlated, trying to search its neural correlates with such crude measures as absolute and relative brain size, in a small sized sample containing different orders of vertebrates, will necessarily be limited in scope. This is all the more problematic considering that this study by Maclean and collaborators represents the state of the art of comparative research in brain and behaviour.

Many anatomical and physiological levels of complexity have not been addressed here. Adding these levels of complexity would be of limited interest, however, if the issues described here at larger levels are not addressed in the first instance. It is also important to note that most of the problems reviewed in this paper are by no mean specific to the papers discussed here, and instead affect most of the literature in comparative neurobiology. Some of these problems are inherent to the multidimensional nature of the field. But most of these issues result from the continuous use of inappropriate methods, concepts and traditions, and are therefore relatively straightforward to address. This requires to improve existing approaches and develop new ones, and also to get rid of some of the hypotheses and approaches that may have historical value for comparative neuroscience and psychology, but that are simply not valid. It also requires abandoning the minimalist approach characterizing most current studies. This kind of research leads to the accumulation of unreliable results that in the end add confusion to a field that has no need for additional complexity.

In addition to the specific commentaries discussed throughout this paper, the framework above permits to propose very general guidelines for using the comparative approach to better understand the evolution of a behavioural ability. In summary:

1. The basic level of analysis should be individuals from a species, populations from a species, or species from a taxon. Comparisons between species and taxa can and should be done, but mixing individuals or populations from different species, or mixing species from different taxa must be avoided or carefully considered.

2. Depending on the analysis, data from a sufficient number of individual/population/species must be collected. Typically when using correlation or regression techniques a number around 30 seems to be reasonable. But more should be always preferred, especially for multidimensional analyses.

3. Data from a comprehensive series of standardized tests aimed at revealing the dimensions of the behaviour should be obtained. Additionally a number of variables potentially relevant, such as those related to mentality (neophoby, general aggressiveness, general activity, etc.). and ecological and social variables must be collected. When comparing species, inter-individual analyses should systematically be carried out in order to reveal sub-patterns (although individuals and species levels cannot be directly mixed). This imposes to collect ad-

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ditional data such as individual differences in the learning pattern, personality, the way the animal approach the test, and if applicable, the place of the individual in the social group for example.

4. Detailed neuro-anatomical data should be collected, at many levels of brain organization (size of the structures, pattern of connectivity, neuron number as well as other measures on neurotransmitters in particular). The use of neuroimagery tools can greatly facilitate this aspect of the study (Mars et al. 2014).

5. Analyses should be conducted among all the variables collected to investigate potential relationships between relative and cumulated effects of the different brain. Each analysis should be examined for potential outliers, and information on these outliers should be used to further study the relationships considered.

What the above suggests is that this level of analysis is for most part out of reach today given the lack of a common objective between researchers of the field. Therefore, new levels of cooperation and data sharing must be implemented. It is important to note that perhaps one of the most rational way for the field to progress would be to focus on the only organisms that present a number of exploitable neuronal and behavioural differences and for which the complete selection pressures can be known: domestic species. Establishing a common and ambitious research strategy should become a priority of the field of comparative psychology and neurobiology.

The arguments presented in Willemet (2013) and discussed in details here provide evidence that important conceptual and methodological changes are needed in the field of comparative neuroscience and psychology. Until this happens, our capacity to study the evolution of brain and behaviour will be undermined.

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