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THE HUMAN BRAIN EVOLVING:

Paleoneurological Studies in Honor of Ralph L. Holloway

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FRONT COVER CAPTIONS

Center: Portrait of Ralph L. Holloway.
Upper left: A modern human brain.
Upper right: Ralph measuring landmarks on an endocast ca. 1976.
Lower right: Homo habilis cranium KNM-ER-1813 from Koobi Fora, Kenya (photo by Holloway).
Lower left: Ralph with an endocast of the Flores "hobbit" cranium.

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CHAPTER 3

THE MEANING OF BRAIN SIZE: THE EVOLUTION OF CONCEPTUAL COMPLEXITY

P. TOM SCHOENEMANN

ABSTRACT

A complete understanding of exactly how to interpret changes in brain size during human evolution remains a major unresolved question. A common misconception is that absolute brain size is not behaviorally relevant, and that only relative brain size (controlling for body size via, e.g., encephalization quotients) has any evolutionary importance. It is argued that this is unlikely to be a valid interpretation of brain size, and that absolute brain size itself is behaviorally relevant, both theoretically and empirically. It is argued that - whatever else brain size increases brought - they likely resulted in fundamental increases in the complexity of conceptual understanding. This, in turn, likely played a central role in spurring language evolution.

INTRODUCTION

The increase in size of the human brain over human evolution is one of the most extensively and clearly documented changes of any species so far documented in the fossil record. Cranial capacity estimates have been made for over 150 separate hominid specimens covering over 3 million years of evolution (Holloway et al., 2004). The increase in cranial capacity indicates a ~3-fold increase in brain volume during this period. Because of the tremendous costs of increasing brain tissue, this increase cannot reasonably be explained as anything other than adaptive (Smith, 1990). The specific costs include the fact that brain tissue is one of the most metabolically expensive tissues in the human body (Hofman, 1983), larger brains take longer to mature (Harvey and Clutton-Brock, 1985), and there is a conflict between the biomechanical efficiencies of narrow hips in bipeds and the need for a large birth canal for increasingly larger brained infants (Lovejoy, 1975). Thus we cannot explain the increase in the human brain without accepting that there must have been some substantial benefit. Presumably this benefit had to do with behavioral abilities, but exactly what was selected for is not clear (Schoenemann, 2006).

BRAIN SIZE AND BODY SIZE

One question that has received considerable discussion regarding the increase in brain size is exactly how to account for body size increases. It has long been known that body size correlates with brain size across mammals, and this has led to a variety of measures of ‘relative brain size’ that take body size into account. The mos t commonly used of these measures is Jerison’s encephalization quotient (EQ), which is simply a ratio of a species brain size divided by the average brain size of a mammal with the same body size (Jerison, 1973). The average brain size of mammals at different body sizes is estimated empirically. Modern humans have EQ’s of between 5 and 7, depending on the mammalian sample used to estimate the average mammal brain/body relationship (Jerison, 1973; Martin, 1981).

Calculating EQ is straightforward, but interpreting species differences with respect to what it means behaviorally is completely unclear. There is an unfortunate tendency in the human paleontology literature for EQ to be treated as if it were something akin to IQ. The assumption seems to be that brain size variation that is explained (in the statistical sense) by body size differences therefore has no behavioral implications. For example, Kappelman (1996), in a paper assessing the possibility of estimating body mass from eye orbit dimensions and thereby allowing EQ estimates of individual fossil specimens, suggests that "…the long period of quite consistent EQs through the nearly 2 million years of premodern *Homo* would predict a pattern of ''behavioral sameness'', which should stand in marked contrast to the behaviors associated with modern humans and their relatively higher EQ." (p. 271). Similarly, Wynn (2002) writes that "Although the brain size of Nariokotome was larger than earlier hominids, so was his body size; there was only a small increase in relative brain size (compared to, say, *Homo habilis*)… It is not clear from the cranial capacity that a significant increase in braininess accompanied this adaptive shift [in the species niche]." (p. 399). And Wood and Collard (1999) write that "Although there are substantial differences in the mean absolute brain size of the australopiths on the one hand and the *Homo* species on the other, some of these differences are almost certainly not meaningful when differences in the body size proxy are taken into account." (p. 69). These researchers seem to believe that relative brain size (EQ or some similar measure) is the most valid criteria for judging behavioral abilities among species of hominids.

Exactly why this assumption is made regarding the interpretation of EQ is usually not explicit. It may be due to a mistaken belief that if brain scales with body, this likely indicates some sort of developmental constraint between them (Schoenemann, 2006). Under this conceptualization, one reason this might be true is that larger bodies might require larger brains to run them with the same level of sophistication. The extra brain mass that is associated with larger bodies (in the statistical sense) therefore isn't available for additional or more complex behavioral functions, because it is completely devoted to simply maintaining the basic functional requirements of the additional body body mass. Kappelman seems to suggest this when he states: "It appears to be the case that many early studies of the tempo and mode of hominid brain evolution focused on brain size only because most workers either assumed that there was no appreciable variation in body mass beyond that seen in modern humans, or that too few data existed to test the question." (p. 268).

The problem with this perspective is that brain size could be associated with body size for reasons other than some sort of developmental constraint, or that a larger body somehow needs a larger brain to run it. It is clear from analyses of brain/body relationships in mammals (and other groups of animals) that species vary tremendously on how much they invest in brain tissue: even at a given body size, the largest mammal brains can be more than 10 times greater than the smallest ones (Finlay et al., 2001; Schoenemann, 1997). This belies the view that body size imposes a tight constraint (developmental or otherwise) on brain size.

A better explanation for the association between brain/body size may be that brain size is constrained – but not determined – by the metabolic resources that are available to a species (Martin, 1981). These metabolic resources are in turn constrained by body size. Because of competition among and within species for survival, species will tend toward the higher end of the possible brain sizes that are supportable given metabolic constraints placed by their body sizes (Schoenemann 2006). This will lead to an association between brain size and body size, but not because they are developmentally or functionally linked. It would also explain the wide range of brain sizes at a given body size in mammals. For some species niches (e.g., those occupied by many primates, and humans in particular), the behavioral benefits of large brains may be more important than they are for other species, and as a consequence, those species would be expected to devote a greater proportion of their metabolic resources to growing and maintaining brains (versus other body components). As a result, brain sizes would tend to vary with body size across mammals (and within other major groups of animals), but with a large range of variation due to the myriad of possible adaptive niches (varying in their cognitive demands) that species find themselves in. Under this model, absolute brain size would actually be expected to be *more* relevant to behavior than relative brain size. Relative brain size would still be important, in that it would index the extent to which a species invests in (or the extent to which a species niche values) brain-related functions. However, under this conceptualization it would be a mistake to assume that species of significantly different body masses are likely equivalent in their behavioral abilities solely because they have the same relative brain size.

At a purely theoretical level, furthermore, there are reasons to believe that absolute brain size is more behaviorally important than relative brain size. First, species with equivalent EQ's but different body sizes (and hence, different absolute brain sizes) do not have (or lack) equivalent numbers of extra neurons (neurons in excess of – or less than, if they have EQ's less than 1 – those predicted by brain/body scaling). Jerison (1973) devised a way to estimate the number of these "extra neurons," based on empirical estimates of the relationship between neuron density and brain size. While Holloway (1974) has cautioned against the uncritical use of such estimates, it is nevertheless clear that, e.g., a large-bodied species with an EQ of 2.0 will have many more extra neurons than a small-bodied species with the identical EQ. For example, using Martin's (1981) body/brain scaling formula for mammals, cotton-top tamarins (*Saguinus oedipus*) have and EQ of ~1.8, which is a bit higher than the EQ of ~1.7 found for common chimpanzees (*Pan troglodytes*). However, in absolute terms, cotton-top tamarins have only ~4 g greater total brain mass than predicted for a mammal of their body mass, whereas chimpanzees have ~167 g extra (which alone is 17 times the size of an entire tamarin brain). From a basic circuit-design/information-processing perspective, it is hard to believe that these species would nevertheless have essentially the same cognitive abilities simply because they have very similar EQ's. To argue otherwise is to believe that larger bodied species need more neurons to accomplish the same sort of cognitive processing, solely because they have bigger bodies. This is analogous to suggesting that radios in dump trucks should be expected to require many more electrical circuits than radios in small cars, solely because trucks are so much bigger. Since brain circuits appear to be very flexible, in that the processing of various cognitive functions can be fairly rapidly shifted to different regions if need be (e.g., 5 days of artificial blindness in normal sighted people learning braille appears to lead to tactile information being processed in the primary visual cortex – which no longer has visual information to process, Merabet et al., 2008), it is hard to see why larger bodies would need more neurons to accomplish the same cognitive functions. Barring some compelling empirical reasons to believe otherwise, our starting assumption should always be that greater numbers of neurons should translate into the potential for more sophisticated cognitive processing.

It is also important to recognize that the evolutionary costs associated with brain size appear to be a function of absolute brain size, *not* relative brain size. The extra metabolic costs of larger brains, for example, are a function of the total mass of neural tissue, not a function of the relative size of this tissue with respect to body size. Using the above species comparison again, chimpanzees have much greater additional metabolic costs for their brains than do tamarins, even though they have about the same EQ. These larger metabolic costs may not require a disproportionately larger share than in smaller bodied animals, since larger bodied species have greater total metabolic resources to draw upon. However, larger bodies also have greater overall metabolic demands generally. If relative brain size is the proper index of behavioral ability, then, everything else being equal, species should evolve towards smaller body sizes to save the metabolic costs (of both larger bodies and larger brains) while maintaining the same behavioral abilities.

Similarly, maturation time is much more strongly a function of absolute brain size than of EQ. Using non-human primate data from Harvey and Clutton-Brock (1985), age at menarche correlates with log brain weight at r=.83 (p<.000001), whereas it correlates with EQ only at r=.59 (p<.00001, EQ estimated using Martin's 1981 equation). Again, two species differing in absolute brain size but with exactly the same EQ would nevertheless likely differ substantially in their average maturation time. Everything else being equal, shorter maturation time is an evolutionary advantage because it translates into more descendents per unit time. If relative brain size really is the proper index of behavioral ability, then species would again be expected to evolve smaller bodies (and hence smaller brains) to reduce maturation time while maintaining the behavioral advantages of the same EQ.

Thus, appropriately smaller body size would be an advantage if relative brain size indexes behavioral ability, because it would allow the species to maintain relative brain size while decreasing the costs of larger brains. It is true that there are independent costs and benefits to body size changes (so reducing body size might have other costs). If behavior is really indexed by EQ, then we have to come up with an independent explanation for the increase in body size during hominin evolution (Kappelman, 1996; Wood and Collard, 1999). However this is complicated by the fact that the increase in body size occurs during a period in which hominins are becoming increasingly independent of their environment through the use of stone tool technology. Increasing behavioral flexibility is generally thought to be the primary adaptation of hominins. If relative brain size really is the appropriate measure of behavioral ability, we should expect, on this account, *decreasing* body size in hominins over time rather then increasing body size, since it would result in lower evolutionary costs while maintaining behavioral ability. However, if instead *absolute* brain size is the better index of behavioral ability, then larger body size in hominins could simply reflect the need to have greater total metabolic resources to help pay for their increasingly large brains.

Ultimately, the question of whether absolute brain size or relative brain size is a better index of behavioral dimensions is an empirical one. Studies of this issue are complicated by the problem of fairly assessing behavioral differences between species. Species differ in both exactly what motivates them (e.g., types of food) as well as in the types of sensory information they focus on (e.g., visual vs. olfactory). If a species fails at a particular task, it might be because it is cognitively limited, but it might also just be because the task favors a sensory modality that isn't the species strength, and/or the species is not properly motivated (Essock-Vitale and Seyfarth 1986; Striedter 2005)? Humans compared to dogs are particularly biased towards the visual domain and happen to particularly favor sugar. A visual task that rewards performance with candy would therefore not be a fair assessment of the inherent cognitive abilities of dogs. This said, there must be *some* reason why species vary in brain size, and if we find some behavioral task that does in fact correlate with aspects of brain size (either relative or absolute), it is useful starting point for hypotheses about exactly why brains differ the way they do across species. Differences in sensory emphases and types of motivation across species are unlikely to result in a purely spurious association with aspects of brain size.

Their are some behavioral associations with relative brain size that have been found. Several studies show significant associations between relative brain size and aspects of diet. Among primates, fruit-eaters tend to have larger relative brain size than leaf-eaters (e.g., Milton, 1988). Bats that subsist on fruits, flowers, meat, fish, or blood tend to have larger relative brain size than bats who are insect-eaters (Eisenberg and Wilson, 1978; Hutcheon et al., 2002). Striedter (2005) suggests the diet-related findings may be explained under a "clever foraging" hypothesis: "…highly encephalized species [those with larger relative brain sizes] tend to forage (or hunt) strategically, taking into account the habits of their food (or prey), while less encephalized species tend to graze (or hunt) opportunistically." (p. 119). Thus, it isn't necessarily the case that hunters are more encephalized than non-hunters. The key seems to be more in the difficulty of finding one's food. For example, it is likely easier for bats to find flying insects than to find fruit, because flying insects are everywhere but fruit is distributed patchily across both time and geographic space (Milton 1988). In some cases relative brain size is more closely associated with some behavioral dimension. While there are some insect-eating bats that have larger brains in absolute size than many fruit-eating ones, the fruit-eaters almost universally have larger relative brain sizes than insect-eating ones (Striedter, 2005).

However, these dietary associations are complicated by the fact that the direction of causality is not clear. Because larger brains place increased metabolic loads on species, it is entirely possible that larger brained species must eat higher quality, more nutrient dense foods to pay these costs (Aiello and Wheeler, 1995). In other words, do the cognitive demands of different types of dietary specializations cause increased relative brain size, or does increased relative brain size occur for other reasons, and simply require certain kinds of foods as a result? The primary metabolic fuel for the brain is glucose, which happens to be found in high quantities in fruits. This could explain part of the tendency of primates with larger relative brain sizes to focus on fruits vs. leaves (though it does not explain, e.g., smaller relative brain size found among insect-eating bats, since insects are fairly nutrient-dense).

Another issue concerns the extent to which broad dietary classes, such as "fruit-eating," are too general as descriptions of behavior to be of much use. There are many types of fruit, and many types of fruit eaters. Fruit-eating would seem to encapsulate a very different level or categorization of behavior than does "problem solving," "behavioral flexibility," or even "3-dimensional spatial recognition." There are likely significant differences in the cognitive demands of various kinds of fruit-eating adaptive niches. Collapsing them all together into a single category leads to such a general level of description as to be helpful only for very coarse levels of understanding. Such correlations are likely of limited value for understanding human brain evolution.

What evidence is there for behavioral correlations with absolute brain size? It turns out that for a large number of studies, absolute brain size is either as good as, or an even better predictor of behavior than is relative brain size (Schoenemann, 2006). Although many studies of brain/behavior associations across primates usually emphasize measures of relative brain size, absolute brain size is invariably also associated with the behavioral dimensions assessed. For example, in Dunbar's (1992) study of 38 primate species, mean group size correlated r=.87 (p<.001) with neocortex ratio (neocortex vs. the rest of the brain), but it also correlated r=.74 (p<.001) with the absolute size of the neocortex by itself. Reader and Laland (2002) similarly showed that the frequency of observations of social learning in 32 primate species correlated r=.69 (p<.00001) with 'executive brain ratio' (ratio of [neocortex + striatum] to brainstem, but that it also correlated r=.58 (p<.0005) with absolute 'executive brain' size (neocortex + striatum) alone. They also found correlations between the frequencies of innovation observed in primate species and 'executive brain ratio' of r=.58 (p<.0005), but also correlations with absolute 'executive brain' size alone of r=.49 (p<.005). Thus, for these aspects of behavior, relative brain size is only marginally more highly correlated than is absolute brain volumes, suggesting that absolute brain size alone is indexing important behavioral variation.

For some particularly interesting behavioral tasks, relative brain size is actually worse than absolute brain size in predicting ability. One example is the speed at which an individual learns that you want it to discriminate between two objects ("learning sets"), and is essentially a measure of how fast they 'learn to learn'. This type of learning task works as follows. First, the subject is repeatedly given the choice of selecting one object out of a pair, with only one of these choices being rewarded in some way (the pair of objects stays the same during this time). When the subject demonstrates that they have learned which object gets them the reward (by consistently selecting this object in subsequent trials), a new pair of objects is then presented, again with only one of them consistently earning a reward. New pairs of objects are introduced as soon as the subject demonstrates they have learned which object of a particular pair is being rewarded. If the subject learns the basic idea behind this task (i.e., that one of a pair will always be rewarded), they learn which object of subsequent pairs is rewarded with fewer and fewer trials. The speed at which the subject gets better at this type of task (learns to learn) can be indexed by assessing the % correct on the second presentation of each set of objects (the first presentation of a given pair can only be guessed at). As the subject learns, their likelihood of selecting the correct object on the second presentation increases. Human children learn this type of task after only a few learning sets (pairs of objects), whereas it takes rats over a 1000 learning sets to approach only ~60% correct on the second trial (50% is guessing randomly, Passingham 1982).

It turns out that this experimental behavioral measure is much more strongly correlated with absolute brain size than it is with EQ. Figure 1 shows the relationships between log learning set slopes (calculated from the second-trial % correct plots) against either log brain size or log EQ (data from Riddell and Corl, 1977). Though the number of species is small (N=11), it is clear that brain size is much more strongly associated with learning set slope than is EQ (though the relationship for both is nonlinear even for log transformed data). Though

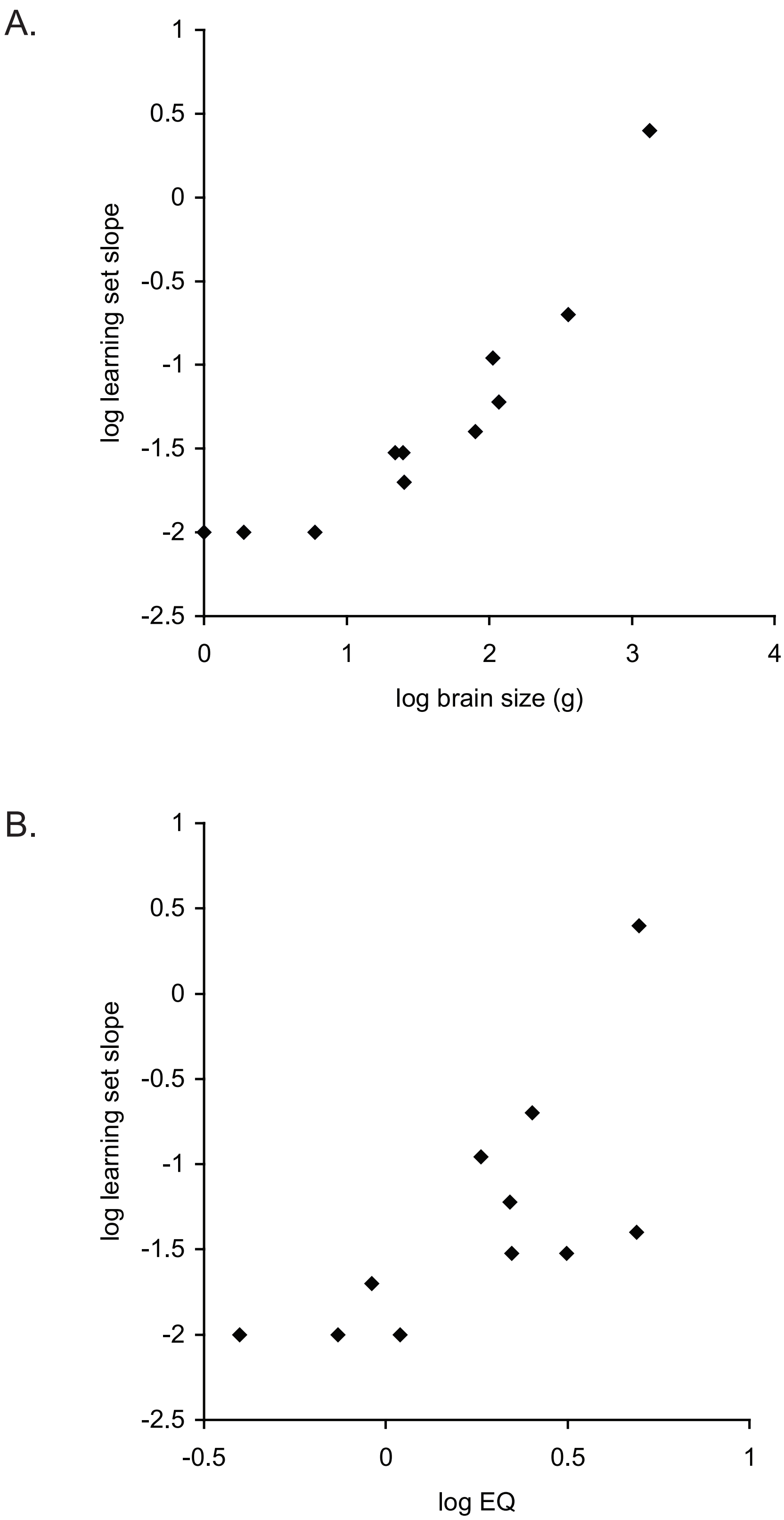

Figure 1: Associations between learning set slope and A. log brain mass (g), B. log EQ. Learning set slope is a measure of how fast a species learns which of two items is associated with a reward. EQ calculated using Martin's (1981) formula. Data from Riddell and Corl (1977). The relationships are nonlinear: [log learning set slope] = .237[log brain size (g)]2 - 2.075, r=.98, p<.001; [log learning set slope] = 2.556[log EQ]2 - 1.761, r=.61, p<.05

it is theoretically possible that some of the differences between species may be due to insufficient motivation and/or differences in sensory emphasis (the learning set studies collected by Riddell and Corl 1977 used visual discrimination), however these differences would then have to independently correlate perfectly with brain size. This is of course possible, but unlikely.

More recently, Rumbaugh and colleagues have devised an ingenious method for controlling for possible cross-species learning confounds (Rumbaugh, 1997; Rumbaugh et al., 1996). Their technique involves training two sets of subjects on a discrimination task, but training them to different levels of accuracy (67% correct vs. 84% correct). The subjects are then tested with the conditions reversed, such that the object that was initially not rewarded now is not, and the object that wasn't rewarded now *is*. The score for a species (which Rumbaugh and colleagues refer to as the "Transfer Index") is the difference between the two groups on their percentage correct for these new, reversed-reward trials. Thus, the measure is insensitive to the total number of trials needed to get to some level of accuracy. Instead, it measures how different levels of learning in a species (however long it takes to be achieved) affect subsequent learning. As such, it is much less sensitive to problems of motivation and/or differences in sensory abilities. For some species, such as the talapoin monkey (*Cercopithecus talapoin*), learning the task to 84% accuracy results in relatively *poorer* performance when the rewards are reversed than if the task was learned only to 67% accuracy. In other words, the better this species learns a to favor a particular object in a discrimination task, the harder it is for it to switch. By contrast, for species such as the gorilla (*Gorilla gorilla*), learning the task to 84% accuracy results in *better* performance on subsequent trials where the rewards are reversed. Gorilla's seem to learn the general idea behind the task, such that they are flexibly able to apply the *idea* of descrimination (as a concept) to a series of tasks, rather than simply learn a series of object discriminations, each essentially disconnected from the rest.

What is particularly interesting about this work is that Transfer Index correlates r=.82 (N=13, p<.001) with the absolute amount of brain a species has in excess of that predicted by their body weight ("extra brain volume", Rumbaugh, 1997; Rumbaugh et al., 1996). It does not correlate significantly with EQ, however. Talapoin monkeys have an EQ of 2.9, whereas gorillas have an EQ of only 1.2 (Schoenemann 1997), for example, yet talapoin monkeys have the lowest transfer index score while gorillas have one of the best scores (trailing only a group of language-trained apes).

Furthermore, a recent exhaustive meta-analysis of the literature by Deaner et al. (Deaner, 2006) show that some species consistently tend to do better across a wide range of behavioral tasks, and that this cannot easily be explained by methodological confounds. Furthermore, Deaner et al. (2007) show that the absolute brain volume correlates most strongly with the relative rankings of general behavioral ability revealed by their meta-analysis. Various measures of relative brain size (such as EQ) were much worse.

Thus, it is quite clear that absolute brain size is strongly associated with important and interesting behavioral dimensions across species. It is important to note that studies of more broad behavioral domains indexed by the size of the social group (Dunbar, 1992) and the tendency towards social learning and innovation (Reader and Laland, 2002) show the highest correlations with EQ, whereas controlled laboratory studies focusing on 'learning to learn' show the lowest correlations. It is therefore not legitimate to ignore or discount changes in absolute brain size during human evolution when assessing behavioral evolution.

This said, it is important to note some caveats. First, not every cognitive domain is necessarily associated with larger brain size. Echolocating bats seem to be able to accomplish extraordinary behavioral feats of sound processing without requiring large brains (or large EQ's). Second, although between-species associations between brain size and behavioral ability presumably require non-zero brain/behavior associations within species, these can be very small while nevertheless remaining highly evolutionarily significant (Schoenemann et al., 2000). Finally, we don't want to forget that there can also be meaningful localized associations between brain anatomy and behavior that likely have played critical roles in human evolution. These constitute part of what Holloway refers to by functional reorganization (Holloway, 1995).

Localized Brain/Behavior Functions

The brain is of course not an undifferentiated mass of neurons, but does have a significant degree of localization of function. This localization appears to be quite flexible, however, as has been revealed by studies of changes in localization of function in individuals who lose a limb or some form of sensory input (e.g., permanent or even temporary blindness as discussed above, see also Ramachandran, 2004). Studies of cortical maps in species with various specialized behavioral adaptations show predictable changes in the relative proportions of particular areas of their cortex (Krubitzer, 1995). Star nosed moles (*Condylura cristata*) have very little need for visual information, as they live most of their life underground, and predictably they have very small visual cortices. About half the cortex of the echolocating ghost bat (*Macroderma gigas*) us devoted to processing sound information (Krubitzer, 1995). This pattern holds even within the human brain: it has long been recognized that the size of various regions of both the primary motor and primary somatosensory areas are proportional to the degree of elaboration of function for a given part of the body. This is usually depicted graphically with a 'homunculus', in which the size of different parts of the homunculus are drawn approximately proportional to the relative size of the corresponding portions of the cortex devoted to those areas.

There are also a few studies suggesting that variation within humans in the size of specific areas of the cortex predicts behavioral abilities mediated by those areas. We have shown, for example, that size of a proxy measure of the prefrontal (i.e., all cortex anterior to the corpus callosum) correlates with performance on the Stroop test of the ability to focus on key stimuli in the face of distractors (Schoenemann et al., 2000). This is consistent with the finding that children with attention-deficit/hyperactivity disorder (ADHD) have smaller superior prefrontal volumes than healthy controls (Hill et al., 2003). More recently, we have found an association between the size of areas of the corpus callosum and behavioral domains in an MRI study of health human females. This work was inspired by Ralph Holloway's many studies of sex differences in the corpus callosum, and his hypotheses regarding its possible evolutionary explanation (de Lacoste-Utamsing and Holloway, 1982; Holloway, 1990; Holloway et al., 1993; Holloway and de Lacoste, 1986; Holloway and Heilbroner, 1992). Specifically, Holloway has suggested that social communication might have been particularly strongly selected for in females, and that this is likely to require more cross-talk between the cerebral hemispheres, but that visuospatial abilities (which males tend to be better at on average) might be better processed in one dominant hemisphere (Holloway et al., 1993). If this is correct, we might expect to find that the mid and anterior portions of the corpus callosum, which connect temporal and frontal lobe areas thought to be important to social domains, would be larger in individuals who are particularly socially adroit. Conversely, the splenium (posterior portion) of the corpus callosum, which connects visual cortical areas and portions of the parietal lobes known to be involved in spatial processing, might be expected to be smaller in individuals who are particularly good at spatial tasks. In a sample of 36 female sibling pairs, we found patterns consistent with this: smaller splenia were associated with better performance on a mental rotation task, whereas larger anterior and mid portions of the corpus callosum were associated with a greater degree of social interaction (specifically: the number of people the subject reported talking to for more than 5 minutes in the last week). Figure 2 illustrates these relationships (unpublished data). These data suggest that localized variation even within species may be associated with behavioral differences.

Thus, both overall absolute brain size, as well as at least some localized neuroanatomical variation, appear to be associated with behavior. Both of these need to be recognized in any complete understanding of human evolution. It should be noted here also that the absolute size of localized regions are likely to be behaviorally relevant *independent* of their relative size compared to other regions, or the rest of the brain. Partly, there is no reason to believe *a priori* that a given circuit is likely to

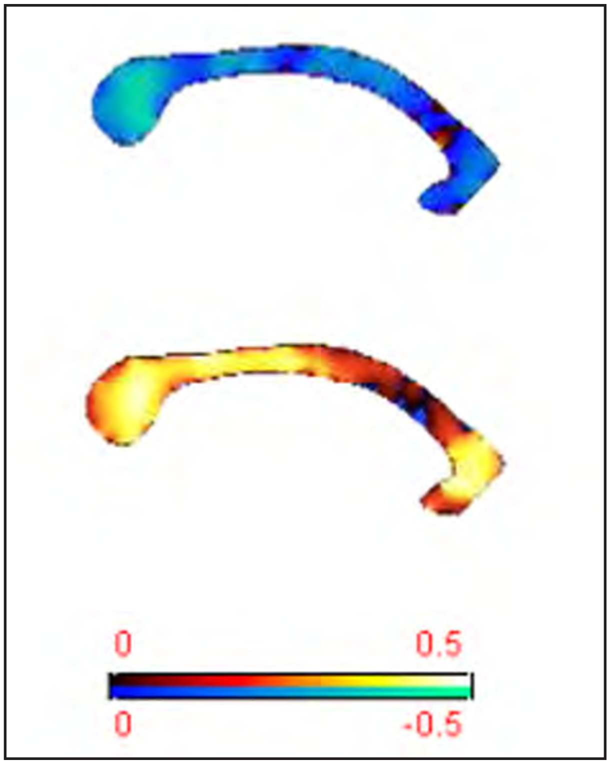

Figure 2: Associations between size variation in cross-sectional areas of the corpus callosum and **A.** *mental rotation ability,* **B.** *degree of social interaction. Black-to-yellow indicate increasingly larger positive correlations; blue-to-green indicate increasingly larger negative correlations. Mental rotation ability is generally negatively associated with localized corpus callosum size, whereas degree of social interaction is generally positively associated. Mental rotation ability was tested using a computerized version of the Vandenberg and Kuse (1978) test. Degree of social interaction was indexed by reported number of individuals talked to in the last week for more than 5 minutes. Localized anatomical variation was quantified using non-rigid deformation techniques (see e.g., Avants et al. 2006). These relationships are correlations of sibling differences in anatomy with sibling differences in behavior, thereby controlling for possible between-family confounds, such as socio-economic status, that might lead to artifactual correlations between anatomy and behavior (Schoenemann 2006).*

work less well if there are more circuits in other regions (subserving other behaviors) than if there are fewer circuits in those other regions. However it is also difficult to square the supposed critical importance of relative area size with the fact that evolutionary costs of neural tissue are a function of absolute size, not relative size. If relative size of a circuit was generally the most behaviorally relevant measure, then species would have evolve very small brains, but with just the right proportions, thereby saving the metabolic and maturational costs but maintaining the behavioral benefits.

Functional Localization as a Consequence of Increasing Brain Size

Comparative studies of brain size differences across species have highlighted an important change that appears to go hand-in-hand with brain size increase. As brain size increases, different areas of the cortex become less directly connected with each other. This appears to be a related to the fact that the number of connections between neurons (or between cortical columns) has to increase much faster than the increase in neurons, if each is to remain equally well connected (meaning: directly connected) to all others (Ringo, 1991). It is structurally much easier for smaller brains to have more direct connections between more areas than it is for larger brains. This fact is reflected in the proportions of white vs. gray matter in different sized brains. White matter consists primarily in connective axons between relatively distant areas, whereas gray matter consists primarily of neuron cell bodies and dendrites. If equal connectivity is to be maintained between neurons, we should expect white matter to increase much faster than gray matter. Empirically, larger brains do in fact have proportionately more white matter than smaller brains, but not enough to maintain equal connectivity among all regions (Ringo 1991).

This has an important general functional consequence, because it means that as brains increase in size, areas are increasingly able to carry out processing independent of other regions. This leads inevitably to functional specialization, in which different areas process different kinds of information in different ways. Empirically, larger brained species have been shown to have larger numbers of distinct cortical areas (Northcutt and Kaas, 1995). Rodents, for example, have only 5–8 visual areas whereas primates have 20–30 (Northcutt and Kaas, 1995). Changizi and Shimojo (2005) showed there is in fact a predictable relationship between the number of distinct, identifiable cortical areas across mammals and a species brain size.

This increase in functional specialization has important behavioral consequences. First, new specialized areas allow for more sophisticate processing of particular types of information. This is an important component of the story, but I wish to focus here on a more general consequence, that operates at a higher hierarchical level of brain function. Specifically, the greater the independence of different areas, the greater will be the sophistication of processing of information overall. Such independence makes parallel processing increasingly possible, and this has significant consequences because it leads to greater sophistication in behavioral response.

Furthermore, ‘actions’ (outputs of various kinds from different areas) can increasingly be separated from inputs. One can imagine a continuum of types of neural circuits, with simple reflex loops involving a single synapse (e.g., startle reflexes that close the eyelids when fast-moving objects approach the eyes) to complex deliberative circuits involving many subunits (functional areas) processing many different kinds of information both serially and in parallel. The later type of circuits are by definition not fast, but they are smart, flexible, and adaptive – the epitome of ‘thoughtful’ processing. Increasing numbers of increasingly separate functional areas inevitably leads to a wholly different kind of behavioral repertoire, that we generally associate with intelligence. Note also that this is a consequence of increasing absolute brain size, not of increasing relative brain size (except, of course, insofar as those two are conflated, as occurred during much of human evolution).

Conceptual Complexity and Brain Size

The concept of intelligence is notoriously difficult to define to everyone’s satisfaction. However, whether or not one agrees that intelligence refers to the degree of complexity of information processing, the increase in the number of quasi-independent processing areas occurring as a consequence of increasing brain size would at least have lead to an increase in the complexity, subtlety, and sophistication of our conceptual universe (Schoenemann, 2005). By “conceptual universe” I mean the totality of all our conceptual understanding, whether it is closely grounded in direct sensory experience (e.g., [hot (temperature)] [water], [ball], etc.), or is more abstract ([evolutionary fitness], [contingent], [love], etc.). Conceptual complexity may be thought of as proportional to the number of independent dimensions the brain can meaningfully distinguish. “Meaningful” distinctions, in this view, would be differences the brain can detect in patterns of stimuli that, in turn, make a difference in how the brain can respond. “Dimensions” are aspects of reality that the species is sensitive to (e.g., chemicals in the air, liquids, or solids, electromagnetic radiation, air pressure vibration, levels of energy, physical pressure, time) as well as internally generated states (emotions, logic, etc.). To see why we should expect brain size to be relevant to this aspect of our cognition, it is necessary to think about how concepts are instantiated in our brain.

Concepts appear to be networks of activation between different areas of the brain, which more or less specialize in particular types of processing of particular types of information. Functional imaging studies support this contention by showing, for example, that passively reading action words that refer to different body parts activates the same cortical areas as does movement of the implied body part (Pulvermüller, 2005). Thus, the concept [kick], brought to mind by the word "kick", activates the areas involved in actually kicking. Similarly, imagining (but not actually seeing) an object often activates the primary visual areas that are active when the object is seen (Damasio et al., 1993; Kosslyn et al., 1993; Kosslyn and Thompson, 2003). Behavioral studies on correlations between different word meanings suggest that the organization of features associated with different word meanings plays a critical role in the organization of semantic memory (McRae et al., 1997). These studies indicate also that information does not flow exclusively in one direction, from primary sensory areas on to secondary sensory and association areas. The activation of primary sensory areas can occur as a result of internally generated activity in other areas of the brain.

Furthermore, even relatively simple conceptual awareness is typically the result of the combination of processing from a variety of cortical areas. For example, our experience of taste is actually the result of the interaction of olfactory (smell) and gustatory (taste) inputs (e.g., banana 'taste' is actually a smell). Auditory perception of simple phonemes is partly a function of concurrent visual input of a speaker's face (McGurk and MacDonald, 1976). Thus, conceptual awareness requires the integration of processing from different areas, and this integration is made possible by neural connections between areas.

It stands to reason that the more processing areas a brain has, the greater the degree of complexity of the possible interactions between these areas. Since conceptual awareness involves activating neural networks connecting different areas, and since larger brains have larger numbers of quasi-independent specialized processing areas, larger brains can potentially create a greater diversity of concepts and a richer and more subtle conceptual understanding. Deacon's (1997) thesis regarding the evolution of symbolic understanding incorporates this idea of conceptual awareness requiring the integration of different neural areas, but he argues that language required an additional step not found in other animals (potentially explaining why other animals don't have language). For Deacon, the key is the ability of conceptual networks to interact more directly with each other, rather than being tied to their grounding in basic sensory information. This would ultimately allow the brain to think entirely conceptually – essentially to form concepts about concepts. Whether or not humans are truly unique in this regard is debatable, but it certainly is clear that human brains have a much greater potential for creating a much greater diversity of conceptual networks.

One simple way to illustrate how simple brain size increases might lead to massive increases in conceptual complexity is to note how fast the logically possible ways of combining different processing areas together increases as a function of the total number of areas. Assume for argument's sake that, as a (gross) simplification, a single concept involves the interaction of a unique subset of n processing areas. The total number of concepts would then be the total number of unique subsets of n areas, which can be shown to be 2^n. This means that the total number of concepts would *double* with the addition of each new area. To put this into context, consider that Changizi and Shimodo's (2005) equation estimating the number of distinct areas as a function of brain size predicts that chimpanzee-sized brains would have ~100 areas, whereas a human-sized brain would have ~150 areas. There are 2^{50} times as many unique subsets of 150 areas as there are of 100 areas.

This simple calculation should not be taken as a straightforward estimate of the degree of difference in conceptual complexity between chimpanzees and humans, of course. For one thing, not every unique combination of processing areas leads necessarily to a unique concept. The concept of [baby] involves such ideas as soft skin and hair (a tactile sensation), small physical size (a visual and/or tactile-pressure sensation), various cries and other sounds (acoustic sensations), and so forth. One would not want to argue that the concept of [baby] necessarily *requires* concurrent activation of all these areas. A species lacking some particular sensory processing area relevant to the human conceptual understanding of [baby] would not necessarily lack the concept of [baby] completely, even though it would clearly be different in some potentially important way. Similarly, the activation of, say, one less area than is typical for the complete concept of [baby] in humans does not constitute a completely unique concept. It would, however, likely be subtly different. The nature of conceptual networks is that activation of a portion of the network usually leads to the activation of the entire network.

Another complication is that, as alluded to above, there appear to be real differences in the complexity of internal processing of particular areas in different species. The pattern for the human somatosensory cortex, in which regions corresponding to parts of the body for which we have more sensitivity are expanded, is a manifestation of a more general pattern across species. Racoons (*Procyon lotor*), for example, have distinct cortical gyri for individual digits on their hands (and relatively large somatosensory cortices generally compared to carnivores), which correspond to their highly developed manual dexterity(Krubitzer, 1995). This indicates that the same area in different species can differ substantially in the complexity of information processing that can be accomplished in given cortical areas. However, the complexity of processing is at least loosely indexed by the size of a given area, and this must translate into a difference in the subtlety and sophistication of conceptual understanding for which that area participates in creating. All of this suggests that the degree of complexity of conceptual understanding can reasonably be considered a function of brain size.

Prefrontal Cortex and Conceptual Understanding

Having many different areas processing many different kinds of information in many different ways is not – by itself – sufficient to produce useful thinking or conceptual understanding. What is needed is a way to organize and prioritize processing from different areas in a meaningful way. It appears that a variety of areas in the prefrontal cortex are specialized for just this sort of processing. The prefrontal cortex also appears to play a general oversight role with respect to processing in other areas of the brain, and in planning generally (Damasio, 1985). Drugs that are used to moderate the symptoms of Attention Deficit/Hyperactivity Disorder (ADHD), such as ritalin, act by making the prefrontal cortex *more* active, for example [they are in fact stimulants, but they are highly specific with respect to what they stimulate cite????]. The prefrontal cortex is also active when learning a new task (Cabeza and Nyberg, 2000), when making any free choice that isn't tightly constrained by the context (Frith et al., 1991; Lau et al., 2004), as well as when experiencing surprising events (Fletcher et al., 2001). With respect to the question of conceptual awareness, areas in the prefrontal appear to be centrally involved in conceptual/semantic information processing (Gabrieli et al., 1998; Gaillard et al., 2000; Kerns et al., 2004; Luke et al., 2002; Maguire and Frith, 2004; Thompson-Schill et al., 1997; Thompson-Schill et al., 1998).

If larger brains tend to have increased numbers of cortical areas, and more cortical areas lead to greater possible complexity of conceptual understanding, and the prefrontal cortex plays a key role in organizing the interactions between these areas, we might expect there to be a biased elaboration in the prefrontal cortex with increasing brain size. Furthermore, since the increase in possible interactions between areas increases geometrically with the increase in areas, we might expect the prefrontal to increase much faster than the rest of the brain (i.e., positive allometry). The evidence in fact supports this prediction. Semendeferi et al. (2002) found positive allometry for the entire frontal (of which the prefrontal is a subset) with respect to the rest of the brain. Our own study found statistically significant positive allometry for a proxy measure of the prefrontal itself (i.e., total cerebrum anterior to the corpus callosum, Schoenemann et al., 2005). This is also true of the cytoarchitectural data from Brodmann (1912), though the data just misses statistical significance (the slope of the regression line predicting log prefrontal cortical area from log non-prefrontal cortical area is 1.13, with 95% confidence intervals ranging from 0.99 to 1.28; N=11, excluding humans). A cytoarchitectural study of area 10, a subset of the prefrontal cortex, in apes shows particularly strong positive allometry (slope of the regression predicting area 10 volume from total brain volume is 1.64, with 95% confidence intervals ranging from 1.16 to 2.12; N=5) (see also Holloway, 2002; data from Semendeferi et al., 2001). Area 10 is particularly important for planning in general (see references in Semendeferi et al., 2001), and is also specifically implicated in semantic processing (word meanings, e.g., Gabrieli et al., 1998; Luke et al., 2002). By contrast, area 13 of the prefrontal, which is more closely associated with aspects of social cognition and not semantic and/or conceptual information processing, does not show evidence of positive allometry in apes, but instead appears to be isometric (slope of the regression predicting area 13 volume from the volume of the rest of the brain is 1.01; N=5, NS). Thus, the prefrontal itself, as well as at least one relevant subdivision – area 10, appears to increase in size faster than the rest of the brain, which is exactly what we would predict given its oversight role organizing activity in posterior areas of the brain.

There is also some evidence that the human prefrontal is particularly enlarged, above that predicted by these positively allometric relationships (i.e., that it got bigger even faster than one would predict from primate brain scaling relationships). Brodmann's (1912) data suggest this (Deacon, 1997), as do studies estimating cortical folding in anterior vs. posterior regions (Armstrong et al., 1991; Rilling and Insel, 1999). Studies estimating the relative increase in size of the prefrontal from studies morphing other species brains in to human brains also support this contention (Avants et al., 2006; Van Essen, 2005; Zilles, 2005). Uylings and Van Eden (1990) do not show increased prefrontal in humans, but their measure of prefrontal is based on thalamic projection patterns, which show much more overlap in smaller brained species, thereby confounding the analysis. The human frontal lobe as a whole (which includes areas in addition to the prefrontal) – although significantly bigger in absolute terms than any other primate – is slightly smaller than primate trends predict (though not statistically significantly so, see figure 2 of Semendeferi et al., 2002). Our proxy of the prefrontal, on the other hand, suggests that humans do have significantly more prefrontal than primate trends predict (figure 4 of Schoenemann et al., 2005). This seems to suggest that, as one looks at increasingly anterior portions of the cerebrum, that humans are disproportionately enlarged beyond even what the positive allometry in primates predicts (see discussion in Schoenemann, 2006).

As the prefrontal cortex plays an oversight role organizing activity in posterior regions, it is not surprising that it has extensive connections to many areas of the brain (Deacon, 1997). Given that larger brains tend to have greater numbers of cortical areas, we might also expect there to be a particular bias with respect to estimates of connectivity to and from the prefrontal. One way to estimate this is through comparing white matter volumes in this region among primates, since white matter contains mostly long-distance axonal connections. Our own study found that the white matter regions of the human prefrontal showed the greatest degree of disproportion compared to primate scaling trends, in fact accounting for most of the disproportion of the prefrontal as a whole (Schoenemann et al., 2005). Schenker et al.'s data (2005) also suggest a disproportionate increase in white matter of the entire frontal (Schoenemann, 2006).

These studies are consistent with the idea that increasing brain size led to dramatic increases in conceptual complexity, and that this required disproportionate increases in the size of the prefrontal over other areas.

Conceptual Complexity and the Evolution of Language

Given that language presupposes a rich conceptual awareness in order to make communication (and/or conceptual ('symbolic') thinking) a useful exercise in the first place, the likely importance brain size increase has for understanding language evolution is straightforward. The connection between increasing conceptual complexity and language evolution has in various ways been pointed out repeatedly, particularly with respect to the role brain size likely has played in this equation (Deacon, 1997; Gibson, 1988; Gibson, 2002; Gibson and Jessee, 1999; Gibson et al., 2001; Schoenemann, 1999; Schoenemann, 2005). The relevance of brain size evolution to language evolution also has a long history, going back at least to Darwin himself (Darwin, 1882; Dunbar, 1996; Nadeau, 1991; Wang, 1991; Washburn, 1960).

Although it has been claimed that the use of natural language syntax and grammar are unique to humans, and that other animals cannot learn them (e.g., Pinker, 1994), descriptions of "universal grammar" (i.e., those grammatical features common to all languages) appear to simply reflect general descriptions of our conceptual universe rather than a series of specific rules (Schoenemann, 1999; Schoenemann, 2005). It is true that individual grammatical rules found in individual languages are often quite specific, to the extent that linguists do not understand how they could be learned without highly specific innate cognitive structures (an argument from "personal incredulity", Dawkins, 1986). However, these are invariably restricted to specific languages, and as such cannot be considered "universal" without special pleading. The features that are universal turn out to be general things like hierarchical structure, rules specifying argument structure (e.g.,: who did what to whom; the specific ways this is accomplished however vary across languages), a noun-verb distinction (which also varies across languages), and so forth (see Pinker and Bloom, 1990).

Because these features appear to reflect our conceptual understanding, they raise the question of whether the rules of syntax and grammar that are supposed to be unique to human language are actually simply cultural manifestations of our underlying conceptual understanding of the world (Schoenemann, 1999; Schoenemann, 2005). Pinker and Jackendoff (2005) seem to suggest this when they state that "...the only reason language needs to be recursive is because its function is to express recursive thoughts. If there were not any recursive thoughts, the means of expression would not need recursion either." (p. 230). Though they themselves believe that recursion in language is not "...a straightforward externalization of a single [internal] recursive system..." (p. 231), this does not rule out recursion's emergence from these apparent conceptual precursors. In fact, a great deal of work, particularly in computational modeling, has suggested that a structure can emerge (in the cultural evolutionary sense) simply from repeated attempts at communication among individuals (Kirby, 2000; Kirby and Christiansen, 2003). Whether this ultimately explains all grammar and syntax found in human languages is an open question, but enough has been shown so far as to make claims that it can't possibly do so obviously premature.

Regardless of one's position on this question, however, language evolution was clearly built on a rich conceptual structure that predated language itself. This in turn appears to owe its existence to the dramatic increase in brain size that occurred during our evolutionary history.

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