14 Human Brain Evolution: History or Science?

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Introduction

In 1998, Robin Dunbar published an influential review of the "Social Brain Hypothesis" (SBH) in the journal *Evolutionary Anthropology*. Although the idea that social complexity played a central role in primate brain evolution had been around at least since the 1960s (Jolly 1966) and gathered considerable support in the 1980s (Byrne and Whiten 1988), it was Dunbar's application of comparative methods from evolutionary biology (Harvey and Pagel 1991) that established the SBH as the consensus view in anthropology and beyond. By operationalizing intelligence ("information-processing capacity") as a ratio of neocortex to rest-of-brain volume and social complexity as average group size, Dunbar was able to show a strong correlation between the two over a wide range of primate species. This was taken as evidence that brain size constrains group size, so that evolutionary increases in group size (for whatever reason) would generate concomitant selective pressure for brain size increase to handle the increase in social complexity. At the same time, Dunbar showed that neocortex ratio was *not* correlated with various measures of ecological complexity (e.g., percent fruit in diet, range size). This straightforward and decisive result convinced many skeptics that social complexity was not merely important, but was almost exclusively responsible for generating the selective pressures leading to primate brain expansion.

Dunbar then went a step further to consider implications for human evolution specifically. This led to what is now popularly known as "Dunbar's Number" of 150: the group size predicted by a modern human neocortex ratio. Although humans obviously have social groupings at various scales of organization, from nuclear families to nations, Dunbar argued that 150 is the approximate number of stable interpersonal relationships a typical human can maintain at any one time. This number is thought to recur in everything from the size of Hutterite farming communities to the length of British Christmas card mailing lists and has even attracted the attention of social media software designers, some of whom are explicitly building "Dunbar's Number" into their systems (Bennett 2013). The success of a hominoid (ape) regression equation in predicting human group size suggests continuity between human and nonhuman primates and supports the view that human brain evolution has been a straightforward extension of a primate trend.

Following this logic, the hominoid regression has also been used to interpolate group sizes for extinct hominin species (using neocortex ratios predicted from whole brain volumes inferred from fossil crania). Aiello and Dunbar (1993) used these interpolated group sizes in combination with comparative primate data on the relationship between group size and time spent grooming to date the origin of language to approximately 250,000 years ago, arguing that increasing hominin group sizes would have necessitated language as a time-saving, "cheap" form of social grooming. Dunbar (2003), using a revised fossil data set, increased this estimate to 500,000 years ago and suggested this earlier date may actually have marked the emergence of "musical chorusing" prior to the development of grammatical speech. Fossil cranial capacities were similarly used to date the emergence of religion (to archaic *Homo sapiens*) based on a correlation between frontal lobe volume and achievable level of intentionality across living catarrhines and the auxiliary argument that supernatural proscriptions require at least level 4 intentionality. Thus, for example: "I have to *believe* that you *suppose* that there are supernatural beings who can be made to *understand* that you and I *desire* that things should happen in a particular way," where italics mark levels of intentionality (Dunbar 2003, p. 177).

These conclusions are stunning. If accepted, they provide specific dates for two of the most evolutionarily significant, hotly debated, and archaeologically invisible events in human prehistory. More importantly, this is accomplished within a single, elegantly simple theoretical framework that explains not just the when, but also the why of these evolutionary events, providing answers to what others have described as evolutionary "questions we will never answer" (Lewontin 1998). The pragmatic power of this comparative, evolutionary biological approach to answer questions that have stymied archaeologists and paleontologists is undeniably appealing. For many, its theoretical emphasis on continuity between humans and other animals is equally attractive and might be seen to place the study of human evolution within a broader, more truly scientific framework. Along these lines, Gowlett et al. (2012) argue paleoanthropology's focus on providing detailed reconstructions of the past has produced a dearth of theoretical content and ceded "big picture" evolutionary interpretation to other disciplines. To remedy this, they propose that a comparative approach based on the SBH can compensate for inherently limited archaeological data:

> If we can understand the broad primate-wide rules that govern the behavior, ecology, and demography of primates (including humans), then we may be better able to identify the sequence of changes that have taken place since the last common ancestor that led, step by (nonteleological) step, to ourselves. (p. 695)

This comparative method is seen as an antidote to a "what you see is what there was" (p. 693) archaeological paradigm unduly limited by the availability of actual material evidence of past behavior.

Obviously, the validity and efficacy of this approach to human evolution depends on the validity and detail of the comparative models that are employed. As one such model, the SBH has led to a great deal of productive research, and this has naturally included important criticisms, extensions, and revisions that must be taken into account and will be discussed below. But there is a more fundamental issue to be considered: Should we in fact expect human evolution to have conformed to “broad primate-wide rules” in the first place? To put it more broadly, to what extent is the evolution of any one particular species actually predictable based on general principles? This is a fundamental and debated question in evolutionary theory that should be addressed by any attempt to apply comparative methods to elucidate the course of human evolution.

Science Versus History?

“Science” means many things to many people, but prediction has a central place in many definitions. Indeed there can be little dispute that the scientific method is fundamentally based upon testing the predictions (i.e., implications) of hypotheses. But it does not stop there. In the natural sciences especially, there is also the idea that one core objective of science is to discover universal laws that allow accurate prediction of physical phenomena. The paradigm example is Newton’s Law of Universal Gravitation: $F = G(m_1 m_2)/r2$. This is a remarkably brief and powerful summary of the way the world works that, among many other things, allowed accurate prediction of the existence and position of Neptune prior to telescopic confirmation. Matt Cartmill (1990, 2002) has argued that scientific (including evolutionary) explanation *requires* an appeal to such lawful “if . . . then” relationships. More specifically, he argues that scientific explanations must combine laws and narratives to form a *modus ponens* argument: “If A, then B (the law); A (the narrative); therefore B (the explained event)” (2002, p. 190). He concludes (p. 194) that if students of human evolution “never go beyond narrative to seek recurrent patterns, then we are not doing science. We’re just telling stories.” Note that Cartmill is not questioning the validity of “historical science” in the conventional sense of using the scientific method to test hypotheses about the occurrence of particular events in the past (Cleland 2002). Rather, he is concerned with the next step of using such historical data to induce generalizable laws of evolution. Although it is not cited by Cartmill, the SBH purports to have identified one such recurrent pattern in primate evolution that can be used to construct properly scientific explanations of human brain evolution and thus to remedy the particularistic storytelling of paleoanthropologists.

Stephen J. Gould was also very concerned to avoid “storytelling” in evolutionary science, but from a very different perspective. Gould and Lewontin (1979) critiqued what they referred to as the “adaptationist programme” in evolutionary biology by asserting the importance of historical and contextual factors such as phyletic heritage, developmental and structural constraint, and (what would later [Gould and Vrba 1982] be termed) exaptation. In essence Gould and Lewontin were questioning the validity of “adaptive optimization” as a universal evolutionary law, and the storytelling they wished to avoid was the uncritical use of this "law" to explain particular traits without due consideration of alternative causes. On the face of it, this might appear to simply be a critique of one particular (putative) law rather than a comment on the nature of evolutionary explanation. However, the underlying philosophical stance goes deeper than that.

Throughout his work, Gould championed the idea of evolutionary contingency. As he (Gould 1995, p. 36) rather bluntly put it:

> Apply all the conventional "laws of nature" type explanations you wish . . . and we will still be missing a fundamental piece of "what is life?" The events of our complex natural world may be divided into two broad realms—repeatable and predictable incidents of sufficient generality to be explained as consequences of natural law, and uniquely contingent events that occur, in a world full of both chaos and genuine ontological randomness as well because complex historical narratives happened to unfurl along the pathway actually followed, rather than along any of the myriad equally plausible alternatives. . . . Contingent events, though unpredictable at the onset of a sequence are as explainable as any other phenomenon after they occur. The explanations, as contingent rather than law-based, do require a knowledge of the particular historical sequence that generated the result . . . many natural sciences, including my own of paleontology, are historical in this sense, and can provide information if the preserved archive be sufficiently rich.

This would seem to be a fundamentally different view on the proper role of generalization, prediction, and law in evolutionary explanation to that espoused by Cartmill. Is Gould's version of contingent evolution really scientific? Or does it simply provide historical narratives of "one thing after another" without any actual explanation?

It seems clear, as Cartmill contends, that scientific explanation must be based on known causal relationships. It is not enough to say that y follows x, we must also say why. Of course this is true of history and narrative as well. Historians don't simply say "Germany invaded Poland and then Britain declared war"; they explain why this particular act produced that particular response rather than another. The point at issue seems to be what exactly qualifies as a "known causal relationship" or law. According to Cartmill (2002), such laws are (1) discovered through the identification of recurrent patterns, (2) universally applicable, and (3) sufficient to allow prediction. To the extent that historical narratives attempt to explain unique events—"Britain declared war on Germany in 1939"—that are not part of a recurrent pattern and could not be predicted from first principles, they should not be considered scientific. Importantly, Cartmill does not deny that such unique events also occur in evolutionary history (and may in fact be commonplace); he merely asserts that these events are scientifically inexplicable. For example, he states (2002, p. 196–197) that "I doubt that we will ever know why our ancestors became bipedal" because human bipedalism is unlike that of any other bipedal animal and must have resulted from "some unique coincidence of factors—some contingency—that does not conform to any recurring regularity of evolution." Such pessimism about one of the core questions in human evolution will not sit well with many paleoanthropologists. Does Gould's approach to contingency offer a viable, scientific alternative?

The positions of Gould and Cartmill are actually closer than either would likely admit. Both recognize that many evolutionary events are unpredictably contingent on particular circumstances, and that explanation requires an appeal to general causal principles. Where they differ is on what counts as a "general causal principle." Gould's best known contributions to evolutionary theory, including work on punctuated equilibria (Eldredge and Gould 1972), evolutionary developmental biology (Gould 1977), and evolutionary constraint (Gould and Lewontin 1979), were clearly attempts to identify recurrent, universally applicable patterns in biological evolution—whether or not he would have been comfortable calling them "laws." The key difference is that these are regularities of process or mechanism whereas Cartmill prefers to focus on regularities of outcome (i.e., convergent evolution). This focus reflects an implicit commitment to the primacy of natural selection as *the* causal principle for evolutionary explanation and restricts the scope of such explanation to recurring adaptations. Dunbar (1998, p. 179) was more explicit about this when he argued that "large brains will evolve only when the selection factor in their favor is sufficient" and that mechanisms other than selection should not be regarded as causal. The implication for Cartmill is that a trait like human bipedalism is unique and inexplicable to the extent that its adaptive function appears different from that of other bipeds. For Gould, on the other hand, an event plus a known mechanism (selective or otherwise) constitutes an explanation, even if the particular outcome is unique and contingent. From this perspective, human bipedalism may be unique in many ways, perhaps including its adaptive functions, but can still be explained in terms of general processes operating in a specific context.

As discussed by Fitch (2012), such an approach to the question of human bipedalism starts with the recognition that " 'Bipedalism' as a monolithic entity is too broad to allow a single, simple causal explanation" (p. 624). For example, bipedal walking and running may have evolved at different times and for different adaptive reasons. Furthermore, each would have evolved from a historically unique set of initial conditions including "the number of leg bones and physiological constraints of bone strength, muscle properties, the rhythm of breathing, and neural control of balance" (p. 624) as well as capacities for phenotypic accommodation that would constrain optimization in some respects while facilitating variation and adaptation in others (Laland et al. 2015). Parallels for aspects of this complex evolutionary process can be found and studied across other species (e.g., biomechanical trade-offs, anatomical plasticity) allowing for a generalizing, comparative, and "law"-based approach. Nevertheless, the particular history of human bipedalism will remain unique. In principle, this is no different than explaining the particular orbital path of Neptune using Newton's Law of Universal Gravitation—it is just that the complex interaction of the causes and conditions involved means the task bears more similarity to explaining the path of a falling leaf in a windstorm.

Clearly, simple explanations are greatly to be preferred where possible, and, regrettably, we remain a long way from explaining the complex evolution of human bipedalism. If human brain evolution turns out to have a simpler explanation than bipedalism, then we would certainly want to take advantage of this. However, we must also remain cautious of the dangers of oversimplification. It is an empirical, rather than epistemological, question as to whether the simplifying and generalizing theoretical framework offered by the SBH is superior to more particularistic and historical archaeological and paleontological approaches.

Problems for Social Brain Theory

Although it is still conventionally referred to as a hypothesis, the use of proposed relations between brain size and social complexity to explain everything from human social structure to the origin of language implies that the SBH actually has the status of an established scientific theory. That is: "a comprehensive explanation of some aspect of nature that is supported by a vast body of evidence" such that it "can be used to make predictions about natural events or phenomena that have not yet been observed" though of course remaining "subject to continuing refinement" (National Academy of Sciences 2008, p. 11). Indeed, decades of research have left little doubt that there is an important evolutionary relationship between brain size and social complexity (variously measured). Nevertheless, there are important reasons to doubt both the causal primacy and universal applicability of this relationship, even if we restrict ourselves to the Primate order where the hypothesis was first formulated. These issues suggest that the SBH may need revision more substantial than "continuing refinement."

Interconnectedness of brain, behavior, and life history variation

The SBH is distinguished from other accounts by its strong claim that the evolution of brain size is driven primarily by the selective pressures of social complexity. In Primates, this claim has been supported by various statistical analyses showing that social group size (as a proxy for complexity) is the best predictor of (relative) neocortex size across an array of ecological and life history variables (e.g., Dunbar 1998, Dunbar and Shultz 2007). The fundamental challenge for this approach is the fact that brain size, body size, life span, developmental length, range size, activity pattern, diet, and sociality are *all* highly correlated with one another as part of species' integrated life history and adaptive strategies (Charvet and Finlay 2012). Using correlation and path analyses to identify one particular variable in this web of complex covariation as causally primary is problematic for two closely related reasons.

First, because so many of the variables under consideration co-vary so closely, comparisons of their relative predictive power will be highly sensitive to differences in error variation within each variable (Isler and Van Schaik 2014). That is, the variable measured with the highest accuracy will tend to be the most successful. Compounding this problem is the fact that many of variables under consideration, including both group size and neocortex size, are actually intended as proxies for something else (social complexity, "computational power"). Thus, we could reasonably expect substantial differences in error variance for both theoretical (e.g., if group size captures social complexity better than percentage of fruit in diet captures foraging complexity) and practical (e.g., if a given variable is easier to measure with precision and accuracy and/or its value is inferred from a larger, more representative sample due to differential research effort) reasons.

One useful way to address such concerns has been to consider a greater range of proxy variables. In addition to group size, social complexity has also been operationalized as number of females in the group, grooming clique size, frequency of coalitions, male mating strategies, prevalence of social play, and frequency of tactical deception, all of which show a relation to relative brain size (reviewed by Dunbar and Shultz 2007). However, a similar effort has not been made to diversify measures of "ecological complexity," or to directly test all of these alternative metrics against one another. When alternative measures of ecological complexity (notably "technical innovation" frequency [Navarrete et al. 2016]) have been included in models, results do not always support the primacy of social complexity as a driving force in Primate brain evolution.

Second, there is the problem of scaling. It is well known that brain size scales with body size across species. What is not well understood are the implications this fact has for the use of various different measures of "brain size" in comparative studies. As Deaner et al. (2000) showed some time ago, different scaling methods (e.g., residuals vs. ratios, scaling to body mass vs. brain subdivisions) produce different results and there is no clear theoretical motivation for preferring one method to another. The SBH is most strongly supported by Dunbar's (1998) preferred scaling measure: the neocortex/rest-of-brain ratio. Other measures generally confirm an association between "brain size" and group size (Dunbar and Shultz 2007, Deaner, Nunn, and van Schaik 2000, Pérez-Barbería, Shultz, and Dunbar 2007), but may not support the strong claims of the SBH that group size is the *best* predictor of brain size (Charvet and Finlay 2012, Deaner, Nunn, and van Schaik 2000) and therefore that "the key selection pressure promoting the evolution of large brains is explicitly social" (Dunbar and Shultz 2007, p. 1345).

An important issue for the use and interpretation of neocortex ratios is that this measure does not control the effect of body size (Dunbar 1992). As Aiello and Dunbar (1993) show, there is a tight correlation between neocortex ratio and total brain size in primates. This is simply a reflection of more widespread brain scaling relationships documented by Finlay and colleagues (Finlay and Darlington 1995, Finlay and Uchiyama 2015, Yopak et al. 2010). Since total brain size scales with body size, it is unsurprising that body size is a good predictor of neocortex ratio (figure 14.1a). This is not necessarily a problem as there are good reasons to suppose that cognitive complexity might scale with absolute brain and

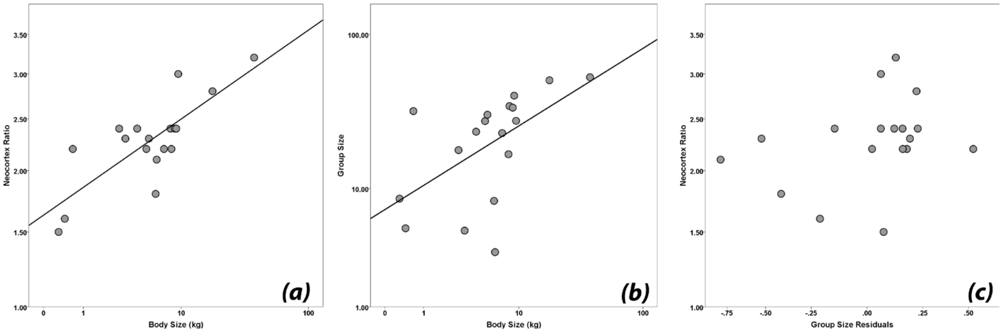

Figure 14.1
Relationships between body size, neocortex ratio (a) and group size (b). There is no relationship between group size and neocortex ratio if effects of body size are controlled using residuals (c). Data from Schillaci (2015).

body size (Deacon 1997). If this is so, rigorously "controlling" for body size would actually remove the effect of interest. However, this positive scaling relationship does need to be explicitly considered in comparative analyses.

For the SBH, it is important to note that body size is also positively associated with group size (figure 14.1b) in all but the largest primates (Janson and Goldsmith 1995). Should this confounding effect of body size be controlled (Schillaci 2015)? Perhaps not, if the association between body and group size is mediated by neocortical constraints on group size (cf. Dunbar and Shultz 2007). However, the actual reasons for body size/group size correlation are unknown and may be ecological in nature (e.g., related to resource distribution, feeding competition, and travel costs [Chapman and Valenta 2015]). An analogous issue confronts the use of range size as a proxy for ecological complexity since range size is also correlated with body size. In Dunbar's (1998) "head-to-head" comparison of range size vs. group size as predictors for neocortex ratio, range size was controlled for body size (using residuals) but group size was not. Not surprisingly, group size fared better. If both variables are treated in the same way (body size controlled/not controlled) the apparent advantage of group size is reduced or eliminated, and range size may appear as a better predictor (e.g., Deaner, Nunn, and van Schaik 2000). In at least one recent data set (Schillaci 2015) a strong association between neocortex ratio and group size ($df=17$, $\beta=0.662$, $F=12.504$, $p=0.003$, $r^2=0.439$) is completely eliminated if group size residuals are used (figure 14.1c: $df=17$, $\beta=0.292$, $F=1.495$, $p=0.239$, $r^2=0.085$).

Theoretically, it is not clear whether one or both proxy variables should be controlled for body size. Do the cognitive challenges of range size scale to "ecological grain effects" that need to be removed (Dunbar 1992)? Or is it instead the case that "bigger is different as far as cognition goes" (Deacon 1997, p. 163). Similarly, is the relation between group size and body size driven by cognitive or ecological constraints? We don't know the answer to these questions, but they inform decisions about appropriate scaling methods that have a huge impact on comparative results. The bottom line, once again, is that all of the behavioral, ecological, and anatomical variables under consideration are intimately connected as elements of species' cohesive life history and adaptive strategies. It is theoretically unlikely that one particular element of this complex web will always have been the primary cause of evolutionary changes in brain size, and attempts to identify such a "key element" are methodologically compromised by sensitivity to differences in data quality and analytical methods.

This brings us back to the issue of "causation" in evolutionary explanation. As alluded to earlier, Dunbar (1998) rejects constraint-based (energetic, developmental) hypotheses of brain evolution by arguing that constraints simply represent obstacles to be overcome by the causal force of selection. Thus, constraint-based explanations "do not do not tell us why brains actually evolved as they did" (p. 179). However, it is clear that selection acts on the actual (net) fitness effects of a trait, and that these are determined by both costs and benefits. The causal reason why "brains evolved as they did" can just as easily be a change in costs as a change in benefits. Thus, the observed pattern of variation across species might in fact be "explained" by constant brain size benefits interacting with variable life history constraints (van Schaik, Isler, and Burkart 2012).

Interestingly enough, Cartmill (2002, p. 197) also makes this suggestion, arguing that "Evidently, bigger brains are advantageous in all sorts of ways of life. . . . So why aren't other mammals as smart as we are? Perhaps they can't afford it." Indeed, the generalized utility of enlarged brains has been supported by research on primate "general intelligence" (Reader, Hager, and Laland 2011, Reader and Laland 2002) and mammalian invasion of new habitats (Sol et al. 2008). This suggests an interesting rapprochement between the universalizing approach of Cartmill and the historicism of Gould: Brain evolution is indeed explained by a general "law" (all else equal, bigger brains are better), but with particular effects that are contingent on a diverse set of context-dependent benefits and constraints. These variables may themselves interact in lawful ways (e.g., Isler and Van Schaik 2014), but with sufficient complexity and sensitivity to conditions that individual outcomes can only really be explained on a case-by-case basis as contingent historical sequences (cf. Gould 1995).

Explaining the evolution of individual species

Another major problem for the SBH is its inability explain apparent "grade shifts" in the relation between social complexity and brain size (van Schaik, Isler, and Burkart 2012, Isler and Van Schaik 2014). The existence of such shifts has been apparent from the outset (Dunbar 1992), and Dunbar (1998, p. 185) suggested that they reflect qualitative differences in social organization such that "apes require more computing power to manage the same number of relationships that monkeys do, and monkeys in turn require more than prosimians do." This argument may in fact be accurate, and it has been extended to explain brain size variation associated with different mating systems across a wide array of mammals and birds (Dunbar and Shultz 2007). Nevertheless, it is an ad hoc accommodation of observed discontinuities in the data and does not provide any causal explanation or predictive criteria for the occurrence of grade shifts.

This is problematic for the SBH in two ways. First, a substantial amount of the brain size variation we are interested in explaining is attributed to grade shifts, and there is no evidence that the forces driving any or all of these shifts were "explicitly social." Byrne (1997), for example, suggested that the discontinuity between apes and monkeys is more likely due to selection on "technical intelligence." In the original data set of Dunbar (1992), this unexplained hominoid shift (+0.83 to intercept) is not much less than the total range of variation in neocortex ratios (1.12) within hominoids.

Second, it is not clear where to draw the line between grade shifts and unexplained residual variation. At the level of individual species, such as unexpectedly large-brained aye-ayes (van Schaik, Isler, and Burkart 2012), these explanations are actually equivalent: The expected relationship has broken down and some additional explanation is needed. In larger, species-rich taxonomic groups, such as the paraphyletic monkey grade (e.g., Dunbar 1998), it is possible to show that a reliable group size-brain size relationship is indeed present (but see previous section regarding interpretation) even if the intercept has shifted relative to other groups. However, problems arise with species-poor taxonomic groups such as the apes. With only three hominoid data points (Dunbar 1998), it is difficult to tell if there really is a reliable correlation ($r^2=0.89$, $p=0.216$). Are we dealing with a grade shift followed by SBH business-as-usual, or has the predictive group size-brain size relationship simply broken down for this taxonomic group? This is a critical point for applications of the SBH to human evolution, as it is the 3-species hominoid regression that is used to predict hominin group sizes (Gowlett, Gamble, and Dunbar 2012).

Unfortunately, there is no way around the paucity of extant hominoid species, but it is at least possible to include two more: orangutans and bonobos. Orangutan neocortex ratio values have been available for some time (e.g., Dunbar 1993) but the species is typically excluded from SBH analyses, perhaps due to uncertainty about the relevant group size. Indeed, recent research repudiates the classic characterization of orangutans as "solitary" and instead recognizes the existence of social "clusters" of related females together with associated males and immatures (Mitra Setia et al. 2009). Here we use a group size value of 31, calculated as the average size (6) of the two female clusters described by Singleton and van Schaik (2002) plus the number of associated males and immatures expected from population sex ratios (ibid.). Group sizes for other species are from Lehmann et al. (2007) and neocortex ratios are from the MRI data of Rilling and Insel (1999).

Regression results (figure 14.2, solid line) fail to show any clear relationship between neocortex ratio and group size (slope: $B=0.084$, $t(5)=0.073$, $p=0.947$; regression: $r^2=0.262$, $F(1, 4)=1.064$, $p=0.378$), and yield a predicted human group size of 62. This suggests that the SBH does not apply to hominoids and cannot be used to predict hominin group sizes, including Dunbar's Number of 150 for modern humans. Of course it is possible that these particular results are unreliable due to inaccuracies in the data sets used. But this is exactly the problem. As discussed previously, the presence of an association between neocortex ratio and group size is robust across data sets and analysis methods but the strength and shape of this association is more sensitive. For example, it has recently been shown that accounting for intraspecific variation in group size can substantially alter regression slopes (Sandel et al. 2016). This calls into question the reliability of model-based predictions for individual species, a problem that can only be compounded by using small numbers of species to predict the extreme values associated with humans. Results obtained here illustrate the fragility of the empirical argument that human brain evolution has been a straightforward extension of a hominoid trend.

In the absence of such empirical support, the SBH provides no theoretical justification for assuming that humans occupy the same "grade" as other hominoids. This is again illustrated by figure 14.2. Even at a glance, it is readily apparent that the regression is heavily leveraged by two species: gibbons (small group size) and gorillas (small neocortex). A reasonable argument could be made for excluding either one (e.g., derived pair-bonding in gibbons, derived cerebellar expansion in gorillas), with major implications for the inferred hominoid regressions (figure 14.2, dashed lines) and human group size predictions (87 vs. 9,913). In essence, these ad hoc accommodations are hypotheses about additional, unpredicted grade shifts (represented by single species) and must be evaluated with reference to arguments and evidence external to the SBH model. Similarly, there is no SBH-internal reason to assume that one or more such grade shifts did not also occur over human evolution, and no way to test the proposition absent detailed archaeological and paleontological evidence of what actually happened in the past.

Archaeology and the Contingent Brain

Any simple regression of real-world biological data can be expected to leave some unexplained residual variation. In the case of the SBH, this residual variation is both substantial and theoretically interesting. While it is possible to address this variation through ad hoc accommodation, as discussed above, the preferable alternative is to develop a more comprehensive model that can support systematic explanations. Such a model might not be simple enough to allow reliable prediction from one or two key variables, but would allow principled explanation of sufficiently detailed individual cases.

Expensive, cultural brains

The most comprehensive account of brain-size evolution currently available is that of van Schaik and colleagues, which brings together two core elements: the "expensive brain" (Isler and Van Schaik 2014) and the "cultural brain" (van Schaik, Isler, and Burkart 2012).

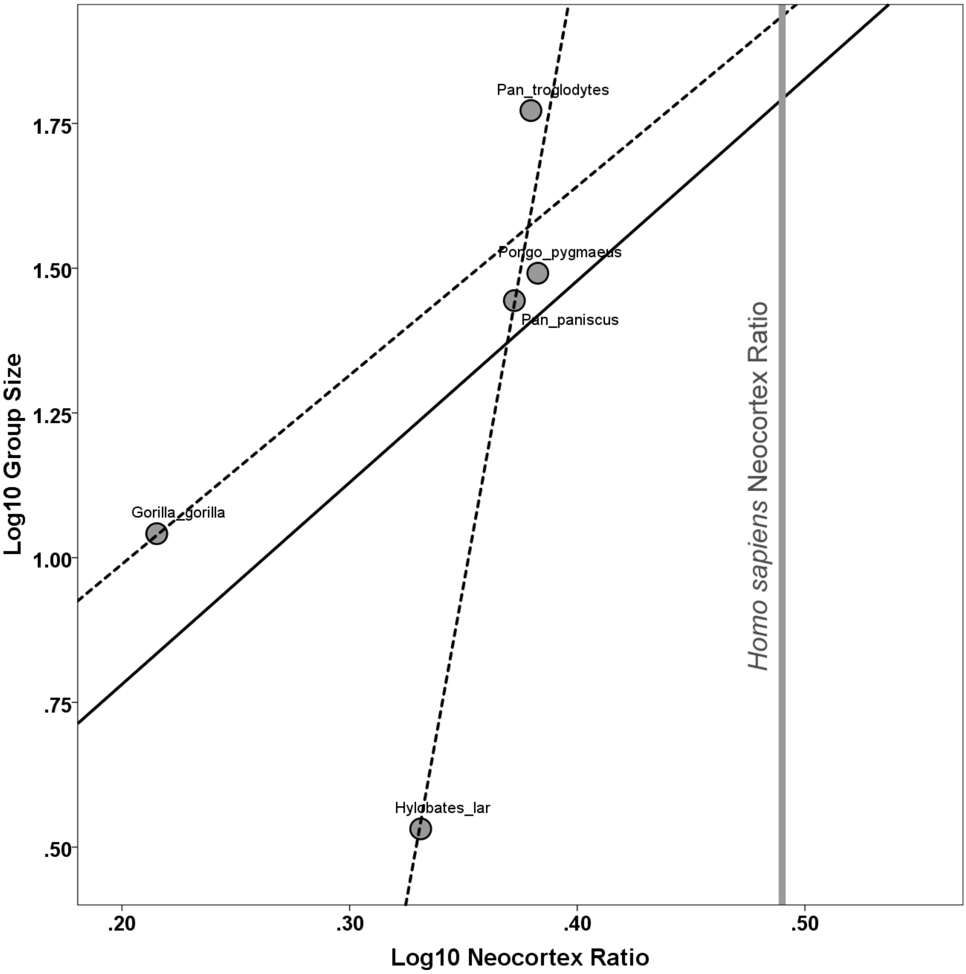

Figure 14.2
Relationship between neocortex ratio and group size in hominoids. Solid line (*n.s.*) is for whole sample, dashed lines exclude either gorillas or gibbons. Grey line indicates human neocortex ratio. Orangutan group size calculated from Singleton and van Schaik (2002); other species as reported by Lehmann et al. (2007). Neocortex ratios are from the MRI data of Rilling and Insel (1999).

The underlying assumption is that, all else equal, bigger brains are generally advantageous (i.e., potentially favored by a large number of different selective pressures). This is supported by comparative evidence of a correlation between brain size and behavioral flexibility or “general intelligence” (Reader and Laland 2002, Reader, Hager, and Laland 2011) and is consistent with the domain-general nature (Duncan 2010) of the large-scale functional networks that occupy much of human (Power et al. 2011) and monkey (Neubert et al. 2014) neocortex. Conserved developmental mechanisms appear to favor the disproportionate expansion of these flexible association networks (Buckner and Krienen 2013, Finlay and Uchiyama 2015) in response to any selection on brain size, which may in turn help explain the convergent evolution of general intelligence (e.g., spanning foraging, sociality, and tool-use) in taxa ranging from birds to cetaceans (Van Horik, Clayton, and Emery 2012). At the same time, the functional plasticity of developing cortex (e.g., Bedny et al. 2011), raises the possibility that even species differences in "modular" abilities (e.g., Amici et al. 2012) may arise through divergent developmental selection (Heyes 2003, Dehaene and Cohen 2007, Heyes and Frith 2014) on more general shared substrates.

Given that any individual could likely benefit in some way from more neural tissue, the "expensive brain" framework seeks to explain interspecific variation in brain size with respect to *net* fitness effects that take energetic and life history constraints into account. Thus, larger brains can only evolve if mortality is low enough to reward investment in slowly developing "embodied capital" (Kaplan et al. 2000) and a sufficient energy budget can be found through increased intake and/or reallocation. Importantly, many of these relationships are inherently multidirectional. For example, brain enlargement initially funded by a shift to a higher quality diet might produce general cognitive benefits with further impacts on both foraging productivity (Genovesio, Wise, and Passingham 2014) and predation avoidance (Byrne and Bates 2007), offsetting metabolic costs, reducing mortality and allowing further brain expansion. Holloway (1967) already emphasized the importance of addressing such feedback or "deviation amplification" relationships in human brain evolution, as well as the difficulty of identifying a primary cause or "initial kick" in such a complex interacting system. An additional implication is that many different causes can have the same effect, so that the long-term trend toward brain expansion along the human line need not imply a similar constancy in selective context.

To this already complex framework, the "cultural brain" (van Schaik and Burkart 2011, van Schaik, Isler, and Burkart 2012) adds the possibility of gene-culture coevolution. Modeling indicates that, if baseline conditions of frequency, learning ability, and skill complexity are met, social learning can increase the mean fitness of a population and lead to cumulative cultural evolution (Henrich and McElreath 2003). This generates yet another potential feedback relationship, in which increasingly complex, socially learned skills both fund and require greater investment in neural tissue, as well as requiring/promoting social tolerance (van Schaik and Burkart 2011), slower life histories, and extensive resource transfers (Kaplan et al. 2000). Humans are seen as an extreme extension of this trend, characterized by reliance on a technological niche (Boyd, Richerson, and Henrich 2011, Stout and Khreisheh 2015, Sterelny 2007) subsiding redistributive "biocultural reproduction" (Bogin, Bragg, and Kuzawa 2014). The cultural brain thus places great importance on sociality but differs from the SBH by explaining fitness benefits within the model (benefits of increasing group size are attributed to exogenous predation pressure by the SBH [Dunbar and Shultz 2007]). More broadly, the cultural brain helps to erode a problematic dichotomy between the "ecological" and the "social" that is difficult to recognize either in the real lives of primates (Rapaport and Brown 2008) or in the brain (Stout 2010).

Implications for the integrated study of human brain evolution

Accepting that there are many possible evolutionary pathways to brain enlargement, it follows that a causal explanation of human brain evolution cannot simply be inferred from its end product. Insofar as outcomes are contingent upon specific conditions, a properly historical account is required. A comparative approach can reveal the law-like regularity of these contingencies, but it is up to the historical sciences of archaeology, paleontology, and geology to provide the narrative element of Cartmill's (2012) *modus ponens* argument structure. This is not to suggest that the aim is to reconstruct a complete, narrative prehistory (cf. Gowlett, Gamble, and Dunbar 2012). Rather, the focus should be on providing rigorous evidence of change through time on the critical contingencies identified by the comparative model. These include brain and body size, diet quality, foraging efficiency, life history, cooperation, sharing, and cultural skill accumulation (Schuppli et al. 2016, Isler and Van Schaik 2014). It is a striking theoretical validation that this list of key issues is nothing new to archaeologists (e.g., Isaac 1971, Washburn 1960). Much remains to be done, but decades of research on these issues have already led to substantial empirical and methodological progress (reviewed by Antón, Potts, and Aiello 2014). Further progress will require ever more thorough integration across the evolutionary and behavioral sciences.

Indeed, evolutionary theory itself has undergone a renovation over the past 25 years, leading to calls for a new, "extended" evolutionary synthesis (Laland et al. 2015). Students of human evolution may now appreciate a broader range of evolutionary processes, including reciprocal causation (organisms as active agents in evolution), inclusive inheritance (more than just genes), and developmental bias (including phenotypic accommodation). This has led to integrated accounts of human evolution that emphasize the role of developmental plasticity, evolvability, niche construction, and cultural evolution (Antón, Potts, and Aiello 2014, Fuentes 2015). Such accounts confront researchers with an increasingly complex web of interacting causes to consider, but also suggest new opportunities for inference from available material remains to the biological and behavioral variables of interest. Examples include links between behavior and plastic anatomical responses (Skinner et al. 2015, Hecht et al. 2015); anatomy, technology, and foraging efficiency (Marzke et al. 2015, Zink and Lieberman 2016); artifacts and socially facilitated learning (Stout and Khreisheh 2015, Morgan et al. 2015, Fragaszy et al. 2013); and development, neuroanatomy, and cognition (Byrge, Sporns, and Smith 2014, Hublin, Neubauer, and Gunz 2015). Particularly promising is the adoption of experimental methods from the behavioral and neural sciences to better understand the implications of reconstructed Paleolithic behaviors (review in Stout and Hecht 2015), and the study of modern individual variation across genetics, anatomy, behavior, and cognition as a window on evolutionary relationships (Bruner et al. 2017, Hopkins et al. 2015, Thornton and Lukas 2012). Formal evolutionary modeling (e.g., Morgan 2016) will be an important conceptual tool as the complexity of interacting processes under consideration increasingly exceeds the scope of informal linguistic arguments.

Despite such causes for optimism, however, we remain a long way from a providing a detailed causal explanation of human brain evolution. Isler and van Schaik (2014) do suggest a plausible scenario in which cooperative hunting assumed major importance in hominin subsistence as early as 2.5 million years ago, leading to improved diet quality and stability and thus to sharing, cooperative breeding, and reduced mortality. This would have initiated a coevolutionary feedback loop between brain, behavior, technology, and life history ultimately leading to the modern human condition. Like Holloway (1967), however, Isler and van Schaik recognize the inherent difficulty of identifying the "initial kick" for such an evolutionary feedback loop. Archaeological evidence of early cooperative hunting is quite scant, being limited to a few cut marks on large animal bones (Semaw et al. 2003, De Heinzelin et al. 1999) and, depending on how big an initial kick we think is needed, we might also consider more subtle causes, such as dietary shifts (Ungar 2012) and/or technology assisted food processing (Zink and Lieberman 2016) as logical antecedents. Given this potential for regress, we may never be able to point to a singular "first cause" of hominin brain expansion. What we can do, and what is ultimately more interesting, is learn quite a lot about the timing, order, and causal relations of the broad span of human evolution. This has been and should continue to be the project of hominin paleontology and Paleolithic archaeology, with a renewed focus on tailoring fieldwork and methodological development to address questions and insights derived from comparative and evolutionary biology. Some high priorities for attention include evidence of cooperative hunting and sharing (Stiner, Barkai, and Gopher 2009), diet quality (Braun et al. 2010), life history variation (Hublin, Neubauer, and Gunz 2015), technological accumulation (Perreault et al. 2013), and the acquisition and social transmission of skills (Stout and Khreisheh 2015).

Conclusion

Sadly, comparative evidence reviewed here does not support a simple, mono-causal explanation of human brain evolution. This does not, however, mean that accounts of human brain evolution are stuck "just telling stories" without scientific content. Rather, it is possible to recognize evolutionary processes as both contingent *and* regular, both narrative *and* lawful. Indeed, it is in the very nature of scientific explanation to combine specific conditions with general principles. The amount of historical detail required depends on the complexity and sensitivity of the causal relations involved, as well as the explanatory detail desired. Since we desire a through explanation of the evolutionary history of a complex trait (brain size) for one particular species (*Homo sapiens*), the level of required detail is high. Fortunately, the historical sciences of archaeology and paleontology have a long tradition of pursuing such detail. If properly informed by progress in comparative and evolutionary biology, continued research in these disciplines will yield increasingly detailed scientific explanations of human brain evolution.

Acknowledgments

Thanks to Adrian Jaeggi for advice on primate comparative data sources and orangutan social structure, to Jeffrey Schwartz, Gerd Müller, Eva Lackner, and all the KLI staff for organizing the workshop, and to the participants for lively discussion.

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