

COMPARATIVE COGNITION & BEHAVIOR REVIEWS

Ingredients for Understanding Brain and Behavioral Evolution: Ecology, Phylogeny, and Mechanism

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Uncovering the neural correlates and evolutionary drivers of behavioral and cognitive traits has been held back by traditional perspectives on which correlations to look for—in particular, anthropocentric conceptions of cognition and coarse-grained brain measurements. We welcome our colleagues' comments on our overview of the field and their suggestions for how to move forward. Here, we counter, clarify, and extend some points, focusing on the merits of looking for the “best” predictor of cognitive ability, the sources and meaning of “noise,” and the ways in which we can deduce and test meaningful conclusions from comparative analyses of complex traits.

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Response

With some notable exceptions, the study of brain–behavior relationships in a comparative, phylogenetic context has been marked by (a) anthropocentrism regarding which behaviors are regarded as important; (b) a focus on coarse-grained neuroanatomical traits, most notably brain size; and (c) a reliance on somewhat slippery notions with contentious definitions like “intelligence” and “cognition.” In our review (Logan et al., 2018), we highlight that brains and behavior are variable, both within species and across taxa. This heterogeneity undermines the use of coarse-grained, anthropocentric measures. Instead, we argue that correlations between neural and behavioral traits in cross-taxa contexts should be tackled using a two-pronged strategy that combines the power of comparative analyses to detect generalizable evolutionary trends, with the depth of understanding provided by detailed studies of ecologically relevant traits in particular species.

Herculano-Houzel (2018) and Serpico and Frasnelli (2018) provide thoughtful commentaries that push our arguments in differing directions. First, Herculano-Houzel (2018) emphasizes the importance of structural variation among brains of different species, particularly in neural number, but questions the two-pronged approach we recommend. Second, Serpico and Frasnelli suggest that we may have been too hasty in dismissing coarse-grained, anthropocentric measures and present a case study in which they argue that such measures are successful. In this response, we wish to emphasize a few points of difference in opinion, clarify our view, and extend the new ideas the commentators have raised.

The studies that interest us establish and explore correlations between neural properties, on one hand, and behavioral or cognitive traits, on the other. We argue that to properly understand their relationships and dependencies, both sides should be considered in finer grained detail. The black box of “brain size” should be opened up to more specific brain structures and neuronal measures, and behavior should be ecologically meaningful and quantifiable. Herculano-Houzel

(2018) focuses on the former point, providing a lucid description of the importance of neuron number. Her view is informed by what she calls “embrained cognitive evolution” (p. 93): the idea that cognitive evolution should be understood in light of within-brain neural structures. She contrasts embrained cognitive evolution with “embodied cognition,” the idea that if we are to truly understand cognition we must not restrict our notions of cognition or investigations of cognitive operations to the vault of the skull. Where the latter asks us to extend cognition to include bodily processes, the former asks us to understand cognitive evolution in terms of internal neural processes.

We wholly agree that embrained cognition is an improvement from focusing on whole brain size or volume. After all, neurons and their synaptic connections play a critical role in producing behavioral phenotypes. We do want to note two points of difference, however. First, Herculano-Houzel (2018) suggests that neuronal number is the best correlate on which to focus, where we recommend a plurality of within-brain correlates. Second, our view is not simply embrained cognition: We also emphasize ecological and phylogenetic context.

For Herculano-Houzel (2018), cortical neuron number is “the best predictor of quantitative differences in cognitive performance across species” (p. 92), implying that it should have priority over other measures. Our view goes beyond choosing one brain measure as a one-size-fits-all variable because we see this approach as making unvalidated assumptions about both the proximate and ultimate basis of behavioral evolution (Logan et al., 2018). The “cognitive performance” to which Herculano-Houzel refers comes from interspecific studies of “self-control” (Herculano-Houzel, 2017; data from MacLean et al., 2014). In our review, we argue that such proxies of cognition are unsuitable for intra- and interspecific correlations (Tables 1 and 2, Logan et al., 2018). Further, despite noting that “cerebral and cerebellar cortices gain neurons in tandem across mammalian species” (p. 92), which *implies* they are functionally interdependent and may both contribute to cognitive evolution (see also Barton, 2012; Barton & Venditti, 2014), the analysis performed in Herculano-Houzel (2017) does not account for this potential interdependence. Moreover, we have argued that the pursuit of the “best” predictor of cognition is itself a mistaken endeavor. Behavior is complex and heterogenous, and as such we may expect a range of variables to contribute to different aspects of behavioral evolution. Treating traits as “predictor” variables implies a strategy for trying to

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deduce cognitive ability from another, more easily quantifiable trait (i.e., using neural number to infer cognitive capacity). We worry that such a strategy is entangled with our desire to rank animals by their cognitive prowess, typically with human performance as the stick against which all others are measured. It certainly does not follow from this that neural number–behavioral correlations (or other correlations) are uninformative, but rather that we should be cautious of this strategy falling into anthropocentrism. Approaching behavioral and cognitive traits from an ecological and phylogenetic perspective, we hope, guards against this.

Herculano-Houzel (2018) suggests that we imply brain size remains a “legitimate” *predictive* variable and instead argues that it should be considered a *descriptive* variable because body mass scales only with some organs, and brain size does not track neuron number in consistent ways across taxa. In our review, we argue that brain size should not be viewed as either a predictive or a descriptive variable but as a variable phenotype. As evolutionary biologists, we should be interested in the proximate and ultimate causes of this variation. We describe how heterogeneity in brain structure and composition differentially effects brain size, and we argue that understanding how brains vary internally is an integral part of understanding brain size variation. The question follows naturally, What determines that internal variation? Answering this requires understanding both developmental aspects of brain evolution and the ultimate selection pressures shaping variation in specific brain components or networks. We do not believe the relatively crude analysis of total brain size and ill-defined behaviors provides an adequate shortcut to addressing these questions.

Herculano-Houzel (2018) contests our suggestion that brain size is a noisy trait and argues instead that it is easily measurable. However, Herculano-Houzel adopts a narrow view of what “noise” is. We defined noise as any feature that affects whether a measurement is transferable outside of the context in which it was measured; that is, “noise” amounts to exogenous confounding effects (e.g., unvalidated proxies leave an open question of whether the behavior of interest was actually approximated; a measured behavior depends on the internal state of an individual and their perception of the environment, which are not accounted for in the behavioral measure; Currie & Walsh, 2018; Logan et al., 2018). When we argue that brain size is noisy, we are not saying that it is difficult to isolate and thus measure, which is a distinct problem, but rather we are pointing

to limitations on the ability of researchers to extrapolate from these measurements; such limitations arise from the exogenous confounding factors endemic in reasoning about complex, evolved systems. Herculano-Houzel’s (2018) argument that the use of brain size as a predictor of cognition is problematic due to variation in neuronal density is therefore consistent with what we have in mind; we think both phenotypic heterogeneity and phylogenetic and ecological context are important sources of noise in studies of brain size.

That aside, we do think brain size is more difficult to measure than appearance suggests: There is a non-negligible degree of measurement error. For example, cetacean species vary widely in the amount of “nonbrain” tissue found within the cranium, which introduces extensive variability when comparing endocranial volume within cetaceans and across mammalian orders (Ridgway, Carlin, Van Alstyne, Hanson, & Tarpley, 2016). Ridgway and colleagues also described how the weight of a brain can change depending on how long it has been immersed in a fixative solution, which is rarely controlled across data sets. These, and other effects such as age and sex, are some of the ways that measurement error can occur and vary in interspecific databases of “average” brain size. Currently, large comparative data sets of brain size are often based on small numbers of individuals; therefore, the extent of these effects on the results of comparative analyses is unknown.

Herculano-Houzel’s (2018) vision for the future of comparative studies of brains and cognition focuses on the emergence of new databases that systematically acquire information on brain composition across species, building on improved methodologies that balance precision and accuracy, particularly in the context of counting neuron numbers. We would happily ascribe to this future, and we are excited about the potential of the field. However, we caution against allowing this kind of analysis to fall into the same old traps—particularly, expecting to find a single brain trait to be the “best” at predicting a behavioral or cognitive variable of interest. We again emphasize phylogenetic and ecological context (see also the “contextual null” in Mikhalevich 2015). We are interested in the kinds of behaviors that make ecological sense for the clade at hand, and the kinds of predictions we make about brain–behavior relationships should emerge from that phylogenetic and ecological context. We must also be open to the possibility that any relationships found may be specific to that context. As such, our approach involves testing the predictions, and understanding the functional basis, of correlations

derived from comparative studies within a target subset of species. Herculano-Houzel objects to this strategy, but she has misinterpreted our argument. She takes it that the two-pronged approach fails to consider scale: interspecies correlations are not invalidated because the correlations don't hold within a species (p. 93). However, we did not necessarily intend for intra- and interspecific correlations to be compared, or for intraspecific studies to be a necessary validation of phylogenetic studies. We suggest in Figure 3 (Logan et al., 2018) that we should use the conclusions drawn from interspecific correlations to generate hypotheses that can be tested within a subset of species, potentially including pairs of phenotypically divergent species, where fine-grained detail can be added to the coarse level of analyses performed in comparative studies. Contrary to Herculano-Houzel's claim that this would require focusing on lower quantitative levels of phenotypic variation, we suggest that the optimal approach would be to target a subset of species that capture the phenotypic or ecological range sampled by a broader comparative analysis. This two-pronged strategy merely reflects a pragmatic trade-off between limitations on the level of functional and behavioral detail that can be collected for each species and the number of species that can be studied.

We would, however, not exclude intraspecific studies of phenotypic variables from this approach. Herculano-Houzel (2018) reminds us that "brains are self-organizing systems that assimilate their environmental and life histories into their structure and function" (p. 93), which may obscure genuine associations between neural and behavioral traits in intraspecific analyses. We acknowledge that plasticity is a key component of neural and behavioral development. However, phylogenetic correlations stem from selection acting on individuals within populations over time. For traits to coevolve across phylogenies, selection must have acted on intraspecific variation at some time in the past; therefore, intraspecific variation in a neural phenotype must be at least partially heritable and have had a fitness/behavioral effect in some ecological context that relates to the results of the interspecific comparisons. Identifying that context in extant populations seems like a legitimate way to follow up on interspecific correlations. But we agree with Herculano-Houzel that failing to find the same interspecific correlations at the intraspecific level does not invalidate the interspecific correlations, in part because the selection pressures and variation in extant populations does not need to be consistent with historical trends. We would also point out that environmental

effects contribute to interspecific variation as well, and may themselves vary over time. This is perhaps a further reason why we should strive to follow up coarse-level phylogenetic analyses with more in-depth study in targeted species. Our point is that we should not be satisfied with simple brain-behavior correlations; we should aim to understand the complex relationship between brains, behavior, and ecology in detail.

In their commentary, Serpico and Frasnelli (2018) argue that the traditional approach (e.g., coarse-grained brain measurements, anthropocentric behavioral traits) can be successful in some contexts. A great virtue of their argument is a shift from considering whether one approach is better generally, to asking how to identify the contexts in which we should expect particular approaches to be suitable or not; building a picture of such expectations fits well with our "no one-size-fits all" approach to brain-behavior correlations.

Serpico and Frasnelli (2018) present the study of brain lateralization as a vindication of the traditional approach. They argue that even though lateralization presents differently across animals, there are nonetheless quite general things to say about asymmetries in brain function at broad phylogenetic levels. We suspect that, rather than revealing the merits of coarse-grained anthropocentric measures, this example potentially demonstrates the merits of combining broad comparative studies with detailed, fine-grained understandings of selected species. The knowledge of lateralization that Serpico and Frasnelli present comes from a functional ("bottom-up") approach that has generated extensive amounts of data from targeted species that display lateralization (see Rogers, Vallortigara, & Andrew, 2013, for examples). This not only resulted in the conclusion that lateralization is a common trait across many taxonomic groups, as opposed to being a human-specific adaptation, but also revealed more about the cellular basis of brain lateralization and its behavioral relevance. To us, this seems like a good example of how the bottom-up approach can build depth into our understanding of a trait whose variation had initially been investigated in coarse detail across broader taxonomic levels.

We argued that understanding both the proximate and ultimate basis of behavioral evolution requires avoiding anthropocentric approaches in favor of framing arguments around the ecological context of the species under study (Logan et al. 2018). Serpico and Frasnelli (2018) view the study of lateralization as a counterexample. We are neither experts nor historians of lateralization, but our impression is that much of this field

was initially driven by a desire to understand variation in lateralization in humans. As such, “success” in this context intrinsically relates to an anthropocentric aim. Nevertheless, as Serpico and Frasnelli note, even though lateralization has subsequently been observed in many lineages, we still do not understand whether this represents repeated independent innovations to a similar problem or whether lateralization inherently arises in all brains, a question we argue could be better addressed by switching to further fine-grained studies in multiple lineages. Finally, although lateralization is not itself a behavior or a cognitive ability, there are potentially ecological contexts in which behavioral variation due to lateralization has significant fitness effects. Understanding these contexts across species would link the study of neural traits, behaviors, and fitness in this example and help elucidate the evolution of the trait of interest.

We are optimistic about our ability to uncover the proximate basis, ecological context, and selective pressures shaping animal behavior and cognition. The field is already progressing at pace via a combination of novel methods of phenotyping behavior and new tools for identifying the genetic and neural variation underpinning behavioral variation. To make the most of these advances, it is time to set aside dated concepts about what brain size means and what cognition is. We should be explicit about assumptions in the field and set out to design ways to test and improve upon those assumptions. When properly applied and contextualized, the combination of detailed bottom-up studies with the potential for a phylogenetic “top-down” approach to test the generality of brain–behavior associations is a powerful route toward understanding brain–behavior relationships in ecologically relevant contexts.

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