

# COMPARATIVE COGNITION & BEHAVIOR REVIEWS

## Embodied (Embrained?) Cognitive Evolution, at Last!

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It is time that brain size stops serving as a black box–type property of brains, “somehow” related to variations in cognitive performance across species. We now know that hidden behind similar brain structure sizes are diverse numbers of neurons and fibers that can differ in function according to experience and environment and that species differences are not a continuation of individual differences. Moving forward in understanding how cognitive evolution is linked to brain evolution requires acknowledging that, just like evolving brains are tied to evolving bodies, changing cognition comes from changing brains—and at multiple levels and timescales, which extend from inherited biological variation to experience and environmental influences that shape each individual brain and turn biological capabilities into actual abilities.

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Cognition was widely considered to be a stand-alone property of brains until Francisco Varela and colleagues formulated the concept of an embodied mind, after which understanding cognition requires taking into consideration several aspects of the body and organism around the brain, from sensory and motor aspects to bodily interactions with the environment (Varela, Thompson, & Rosch, 1991). Corina Logan and colleagues make a similar appeal to those of us interested in studying brain evolution and its implications for cognition: that there can be no real understanding of cognitive evolution without a preoccupation to take into consideration the diverse makeup of the brain (and the rest of the body), as well as the neuronal basis of the behavior and the ecological context for the species in question.

The authors are conservative when they state that progress ahead will lie in acknowledging the diversity of brain morphologies and behavioral capacities

and focusing on specific neuroanatomical and behavioral traits within relevant ecological and evolutionary contexts. Because one of the advantages of writing a commentary is that I don't have to be as conservative, I would like to go further and suggest that what they propose amounts very much to the evolutionary version of embodied cognition, or how embodied cognition evolves over geological time. Their proposed “shift away from broad-scale analyses of superficial phenotypes” can be understood as requiring exactly the type of analysis that depends on what the relevant circuits underlying a given behavior (or cognition as a whole) are made of and describing how they fit in a species' brain and ecological niche. “Embrained evolution” would thus be a fitting term for their proposed strategy for understanding how cognition compares across species and how those differences evolve—as opposed to so many of the past strategies that just glaze over what brains are made of, as if that were an unnecessary inconvenience.

In a field that has been riddled with implicit assumptions about what brain size measures and how it correlates with behavioral and cognitive traits (such as the equally ill-defined “intelligence”), Logan and colleagues make a lucid attempt to spell them out and understand the progress, but also the confusion, that those assumptions have brought. Take brain size, for instance. For decades, this was understandably the most practical morphological measurement of anything brain related, but its use was based on the initially explicit (Jerison, 1973) but then progressively more hidden assumption that absolute brain volume and relative volume of brain structures stood universally for absolute and relative numbers of neurons composing the brain and its structures. The hidden assumptions, and the fact that they were obviously incorrect, as later data attested (Herculano-Houzel, 2010, 2011a, 2011b), explain major contradictions in the interpretation of results such as the faster scaling of cerebral cortical over cerebellar *volumes* across species (Clark, Mitra, & Wang, 2001), whereas their *surface areas* scale only linearly across the same species (Sultan, 2002). Assuming implicitly that (relatively and absolutely) larger cortices are made of (relatively and absolutely) more brain neurons than larger cerebella, Clark et al. (2001) inferred that the cerebral cortex comes to dominate brain function as larger brains evolve; conversely, and using the same data set but assuming instead that it is surface area that reflects the number of neurons and hence the information-processing capacity of cerebral or cerebellar cortical structures, Sultan (2002) concluded that the two structures gained in processing capability concertedly in evolution. Both can obviously not be true at the same time. So which is it?

Neither, it turns out; being able to estimate numbers of neurons directly, without making assumptions about the volume or surface area of the brain structure they compose, allowed us and our collaborators to determine that there is not a universal relationship between the volume of a cortical structure or its surface area and the number of neurons that compose the structure (Herculano-Houzel, 2010; Jardim-Messeder et al., 2017; Mota & Herculano-Houzel, 2015). Now that absolute numbers of neurons are available and can be compared directly across equivalent structures in different species, the

picture that emerges is one in which cerebral and cerebellar cortices gain neurons in tandem across mammalian species, regardless of the two-dimensional or three-dimensional size of the structures, and in which absolute numbers of cortical neurons appear as the best predictor of quantitative differences in cognitive performance across species (Herculano-Houzel, 2017). Most of the data generated so far have been concerning whole structures that are easily definable in a comparable fashion across species (whole cerebral cortex, whole cerebellum, whole olfactory bulbs). But, as those data lay a new foundation that is increasingly consistent in the story it tells, and as the method employed gains traction in the field as comparable in precision and superior in ease of use to stereology (Herculano-Houzel, von Bartheld, Miller, & Kaas, 2015), the numbers of neurons that compose functionally or anatomically identified brain structures are expected to become increasingly available in larger numbers of species. It is the hope of some of us in the field that the growing availability of these data, as well as manifestos such as that of Logan and colleagues, will drive more and more researchers to no longer consider themselves satisfied with reporting just brain size in the species they study, and instead to expand their analyses to systematic investigations of numbers of neurons (or cell subtypes, connections, synapses) in the behaviorally relevant structures across species. In this manner, I hope the day will come soon when databases emerge with systematically acquired data on brain structure composition that can be cross-correlated to behavior across species with as few assumptions as possible standing in the way of understanding the cognitive consequences of brain scaling in evolution.

So far, it has become clear already that normalizing morphometric features for body mass, a procedure that was meant to eliminate common factors, actually introduces more noise to the analysis (Herculano-Houzel, 2017). Using residuals after correction for body mass rather than absolute values was a rescuing measure prompted by the vexing realization that neither the human brain nor its cerebral cortex was the largest of them all (Jerison, 1973; Stephan & Andy, 1964), but it turns out to warp data in a manner that “favors” the relatively small bodied—when body size may actually not be relevant for cognition. Instead, it turns out that regardless of body size or even brain size, humans have the most neurons in the cerebral cortex, and crows and large parrots have just as many neurons in their relatively tiny pallium (the corresponding structure, albeit nonlayered) as the much larger brained and larger

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bodied macaques—findings that make sense with their otherwise unexplained similar cognitive abilities (Emery & Clayton, 2004).

I do disagree with Logan et al. in some points. Although the authors spell out many assumptions about brain size that have turned out to be wrong, they still refer to it as a legitimate variable, which I argue it's not—no more than body mass is informative of its parts, which is to say, really not. Although some organs scale at fairly constant proportions to others (i.e., isometrically), many are largely free to vary, which makes body mass only appear to be a good proxy for body composition (Herculano-Houzel, 2018). Similarly, it must be acknowledged that the size of the brain is the result of its parts—how many neurons of what average size in what structures—and because the parts are to a large extent free to vary in both numbers of neurons and average cell size across species and clades, brain size is not a good universal predictor of how many neurons compose each brain part (Herculano-Houzel, Catania, Manger, & Kaas, 2015; Herculano-Houzel, Manger, & Kaas, 2014). Thus, rather than proposing that “understanding how brain size relates to selection for behavioral complexity or cognition is . . . a two-step process” (Logan et al., 2018, p. 59), I would urge readers to keep using brain size as a descriptive variable, of course, but consider eliminating it as a *predictive* variable altogether.

I also disagree when the authors state that brain size is a noisy variable. It is very easily measurable with high reproducibility across measurements, which makes it far more precise than, say, our best direct estimates of numbers of neurons (which typically come with a method-defined coefficient of variation of 5%). What is noisy is how brain size has been used as a variable: as a direct measurement, an indirect estimate, or a proxy for something else; compared across multiple clades together, as if accounting for phylogenetic relationships were enough to separate what turn out to be clade-specific relationships; or compared across individuals of the same species and sometimes simultaneously across species as if variation in either case amounted to the same thing.

This latter assumption, by the way, takes me to my final commentary. Logan et al. suggest a two-pronged approach to comparative studies of cognition, in which the first prong is comparing behavior and how it relates to brain composition across individuals within same species. The underlying logic is the expectation that whatever variations turn out to be relevant for predicting differences in behavior across species (or ultimately

causative) necessarily must also apply across individuals of a same species. The first and most obvious problem with this logic is one of failing to consider scale: Almost by definition (domestic dogs excluded), variation is orders of magnitude larger across species than across individuals of the same species, so the opportunity to detect significant correlations in a small range (the species) is much smaller than across a large range (across species) even if it could be ascertained that they are manifestations at different scales of the same underlying phenomenon. For instance, so far the strong correlation across species between structure mass and the number of neuronal or nonneuronal cells that compose it is not replicated across individuals of the same species (to the contrary, the opposite pattern emerges in how cell density scales with cell number; (Herculano-Houzel, Messeder, Fonseca-Azevedo, & Pantoja, 2015), but that lack of a significant correlation between structure mass and number of neurons across individuals certainly does not invalidate the obvious correlation detected at a larger scale.

Second, and most important, is the problem of failing to consider that brains are self-organizing systems that assimilate their environmental and life histories into their structure and function. Although brains (or hippocampi, or olfactory bulbs, or superior colliculi) with a twofold difference in numbers of neurons could be expected to differ in their information-processing capacity across two species, two individuals of the same species with identical numbers of neurons in the relevant structures may have had their behavior so dramatically shaped by opportunity, practice and any other number of factors that, although they have similar information-processing capabilities, their actual behavioral *abilities* differ in ways that couldn't be predicted from their numbers of neurons. A two-pronged approach such as that proposed by Logan et al. is thus fine as long as it does not expect one prong to be a natural extension, or continuation, of the other. Besides embracing a program of “embrained cognitive evolution” that takes brain makeup into consideration, I would urge that comparative and evolutionary studies of cognition start taking great care in separating what are biological *capabilities*, dependent, for example, on numbers of neurons, or synapses, or connecting fibers, and what are behavioral *abilities* that incorporate opportunity, innate genetic/physiological variation, environment, and culture, and thus reveal those self-organizing properties of the brain that allow it to assimilate external information into its complexity (Herculano-Houzel, 2016).

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