COMPARATIVE COGNITION & BEHAVIOR REVIEWS

Where the Standard Approach in Comparative Neuroscience Fails and Where It Works: General Intelligence and Brain Asymmetries

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Although brain size and the concept of intelligence have been extensively used in comparative neuroscience to study cognition and its evolution, such coarse-grained traits may not be informative enough about important aspects of neurocognitive systems. By taking into account the different evolutionary trajectories and the selection pressures on neurophysiology across species, Logan and colleagues suggest that the cognitive abilities of an organism should be investigated by considering the fine-grained and species-specific phenotypic traits that characterize it. In such a way, we would avoid adopting human-oriented, coarse-grained traits, typical of the standard approach in cognitive neuroscience. We argue that this standard approach can fail in some cases, but can, however, work in others, by discussing two major topics in contemporary neuroscience as examples: general intelligence and brain asymmetries.

Keywords: general intelligence, brain asymmetries, comparative neuroscience

What do coarse-grained and taxon-neutral traits, such as brain size and intelligence, tell us about neurocognitive systems? What characteristics should a behavioral proxy have to allow us to properly compare cognitive abilities across different taxa? In their article "Beyond Brain Size: Uncovering the Neural Correlates of Behavioral and Cognitive Specialization," Logan and colleagues address these questions by reviewing the literature on the relationship between brain size and cognition. In the light of empirical and theoretical considerations, the authors suggest that, to understand how brain and cognition evolve, comparative biologists should focus on fine-grained, taxon-specific phenotypic traits within the relevant ecological and adaptive context

of a given species. This would help to avoid reification, defined by the authors as mistaking an operationalized target of measurement with a real, causally meaningful object.

Although we agree with this conclusion, there are two aspects analyzed by Logan and colleagues that we think may deserve further consideration. The first is the common tendency in comparative research to assess human-oriented phenotypic traits in nonhuman species; the second is the tendency, which is also widespread, to adopt coarse-grained traits, such as brain size, instead of fine-grained and more informative traits.

Let us start by considering the first one. A general premise of Logan and colleagues' article is that

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comparative behavioral research is often characterized by a sort of "anthropocentric perspective." However, as the authors argue, human behavioral traits—and the related neural bases—are not necessarily shared by other species. This argument can be understood as a criticism against the so-called Great Chain of Being, a secular ideology that assumes a natural hierarchy of organisms with humankind at the top and then, successively, lower animals from primates to bacteria (see, e.g., Sternberg, 2017). Logan and colleagues clarify how misleading this interpretation of the tree of life is by highlighting the importance of the ecological and adaptive context of a species: The ability of the organisms to achieve their goals should be evaluated within the range of challenges they face within their natural environment. Therefore, phenotypic traits should be identified by accounting for what is actually "meaningful" for a given species rather than what is meaningful for humans.

The second central point of the target article concerns the use of general, coarse-grained phenotypic traits and proxy measures to study cognition. Brain size represents, in the authors' view, a noninformative measure of neurocognitive systems. Indeed, such a broad measure cannot disentangle from one another important aspects such as the dimensions of specific brain areas, the neuron density, and the connectivity patterns between neurons, which may be more informative than brain size about the properties of a neurocognitive system. Hence, it is not surprising that correlational analyses of brain size tend to produce spurious associations at both the intraspecific and interspecific levels (reviewed by Logan et al.).

We recognize that these criticisms could rule out misleading assumptions in comparative behavioral research. However, although the authors' arguments seem to be applicable to most research about high-level psychological constructs, we believe they may miss the mark in respect with structural features of nervous systems and the related behavioral manifestations. To explain our concerns about the approach proposed by Logan and colleagues, we use as examples two topics

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in neuroscience: general intelligence and brain asymmetries. These two examples elucidate where the coarse-grained and human-oriented comparative approach fails and where instead it can be appropriate and helpful.

The authors' argument against anthropocentric comparative research sounds effective in the case of general intelligence and its putative underlying mechanism, namely, the g factor. General intelligence represents a psychological trait assessed by psychometric IQ tests that generally recruit linguistic, mathematical, logical, and spatial abilities. The g factor, instead, is often understood as a domain-general cognitive mechanism accounting for both individuals' performance in tests (i.e., the intelligent behavior) and individual intellectual differences within populations (see Burkart, Schubiger, & van Schaik, 2017; Serpico, 2017; Sternberg & Grigorenko, 2002). General intelligence is the subject of heated controversy in regards to two aspects tackled by Logan and colleagues with respect to brain size, that is, the granularity problem and the anthropocentric perspective widespread in comparative research.

First, exactly like brain size, general intelligence represents a coarse-grained evaluation of a cognitive system, regardless of any detail about its structural and functional composition. However, many scholars have argued that intelligence, rather than reflecting a single neurocognitive mechanism, is composed of several distinct and autonomous—but not necessarily independent—cognitive mechanisms (see Hampshire, Highfield, Parkin, & Owen, 2012; Serpico, 2017; Sternberg & Grigorenko, 2002; Van der Maas et al., 2006). Logan and colleagues' argument about brain size is in line with the view that general intelligence, like other high-level psychological constructs, does not represent an informative measure of neurocognitive systems (see Craver, 2009, who discussed the problem of subtyping complex psychological traits into lower-level characteristics).

Second, we think that general intelligence is exactly that sort of human-oriented trait that Logan and colleagues criticize as erroneously generalized to other species. Although the g factor likely plays a role, if any, in human cognition only (indeed, g accounts for the population variance in a battery of IQ tests), many authors have tried to assess its role in other species. For instance, in their review about the evolution of general intelligence, Burkart and colleagues (2017) took the g factor as a domain-general neurocognitive mechanism shared by humans, primates, birds, and rodents. The arguments provided by Logan and colleagues against

the anthropocentric viewpoint in comparative studies seem to us well suited to describe, and possibly to rule out, this sort of reification of general intelligence.

By contrast, the arguments provided by the authors seem to be less suited to be applied to structural properties of nervous systems. This is the case of brain and behavioral asymmetries, where a sort of human-oriented, coarse-grained approach seems to be promising and successful.

Traditionally, lateralization (i.e., the different functional specialization of the right and left sides of the nervous system) was considered a uniquely human characteristic, related to handedness and linguistic functions (McManus, 1999). Over the past decades, thanks to research conducted in comparative psychology, neuroscience, and developmental biology, we have realized that lateralization is a widespread phenomenon among vertebrates (Rogers, Vallortigara, & Andrew, 2013). Moreover, there is emerging evidence of behavioral and brain asymmetries in invertebrates, suggesting that lateralization is a feature of simpler as well as more complex neurocognitive systems (reviewed by Frasnelli, 2013).

In most vertebrates, for example, the right hemisphere is involved in responding to unexpected and novel stimuli (e.g., predators) and in interacting with conspecifics, and the left hemisphere is specialized in less complex and repetitive tasks (e.g., behavioral routines). Lateralization also characterizes learning and memory both in vertebrates (e.g., in birds; see Andrew, 1999; Cipolla-Neto, Horn, & McCabe, 1982; Clayton, 1993) and in invertebrates. For instance, honeybees present an asymmetrical use of the right and left antennae in learning and recalling olfactory memories: recall of short-term memory is implemented by the right side, whereas recall of long-term memory is possible through the left side (see Letzkus et al., 2006; Rogers & Vallortigara, 2008; for a review, see Frasnelli et al., 2014). This suggests that the shifts between the two sides of the brain from recently acquired information to more integrated and complete long-term records might constitute a considerable advantage for both arthropods and vertebrates. Thus, mechanisms controlling such shifts may have evolved, perhaps independently, in both phyla (see Frasnelli, Vallortigara, & Rogers, 2012).

In sum, despite differences between the nervous systems of humans and other animals, there is good evidence that lateralization represents a structural feature implemented by similar mechanisms across different species and taxa (see Rogers et al., 2013). Thus, thanks to these similarities, animal models have allowed

us to uncover the evolution of behavioral and neural asymmetries, and their developmental mechanisms as well.

The take-home message is that the approach proposed by Logan and colleagues might be promising for behavioral traits reflecting higher-level cognitive aspects such as general intelligence but be potentially fragile for behavioral traits reflecting lower-level structural properties of the nervous system. As we have argued, the disagreement about general intelligence relies on its generality and on its dubious value in characterizing the neurocognitive system of nonhuman species. By contrast, what we know about lateralization points at the (partial) adequacy of a human-oriented, coarse-grained approach in comparative research.

We do not mean to assume an anthropocentric view-point. Nevertheless, there are good reasons to think that some structural aspects of nervous systems—and their behavioral correlates—are highly conserved across different taxa, regardless of their granularity. Whether the conservation of this kind of traits is due to natural selection, to the modularity of the related genetic processes, or to some sort of developmental constraint in brain morphology is an empirical question that future research must address.

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