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Individuating Cognitive Characters: Lessons from Praying Mantises and Plants

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Abstract

This article advances the development of a phylogeny-based psychology in which cognitive ability types are individuated as characters in the evolutionary biological sense. I explain the character concept and its utility in addressing (or dissolving) conceptual problems arising from discoveries of cognitive abilities across a wide range of species. I use the examples of stereopsis in the praying mantis, internal cell-to-cell signaling in plants, and episodic memory in scrub jays to show how anthropocentric cognitive ability types can be reformulated into cognitive characters, thereby promoting the integration of psychology with other sciences of evolved traits.

1. Introduction

This article advances the development of a phylogeny-based psychology, in which cognitive ability types are individuated as characters in the evolutionary biological sense explained in the following text.¹ A phylogenetic perspective draws attention to a key question for psychology: How does the extension of a cognitive concept or category to a new species affect the way we define that concept or category?² This question lies behind many of the conceptual and related empirical debates raised by

¹ Section 2 explains these concepts. I use “cognitive sciences” and “psychology” as synonymous despite the strong association of psychology with humans other than in the tiny subfield of “comparative psychology,” which is essentially synonymous with “animal cognition.” My linguistic choice reflects the view that the conceptual foundation of psychology as a whole should be as comparative as that of biology. “Ability” is used broadly to include capacities, dispositions, states, processes, or other ontological types.

² Unless expressly indicated, the differences between categories, concepts, and terms will not matter here: I will assume concepts pick out categories and are denoted using category terms. Similarly with categories, kinds, and types—differences among these will not matter. Thus, while Kendig (2016) helpfully explores “kinding” practices in biology, my interest is specifically “character-ing,” not “phenotyping”—reference to “kinds”, like “traits”, can obscure this key difference.

reported findings of advanced cognitive capacities across more species, including many that are not human-like at all. A particular way of answering it yields a phylogenetic psychology, which eschews traditional cognitive types based on human phenotypes in favor of the character-based individuation scheme used in other sciences of evolved traits.

I begin in section 2 by explaining the importance of the character concept in evolutionary sciences in general and its potential for clarifying psychological concepts and research questions. In section 3, I introduce the general problem of individuating cognitive characters given our anthropocentric starting point. I then elaborate two case studies of proposed revisions of noncognitive character concepts. These cases highlight the impact on character individuation of the extension of a character to new species—a situation we face in spades for cognition. In section 4, I critically discuss a proposed redefinition of the concept of stereopsis based on research with the praying mantis. This case reveals the critical role of the phylogenetic position of a species and how structural and functional characters are integrated. In section 5, I consider a proposed redefinition of the concept of a nervous system based on research with plants. This case adds the impact of multiple levels of biological organization on individuation and taxonomy decisions at any given level. In section 6, I use the case of episodic memory to show how discoveries in new species motivate revising a human-centered concept into a cognitive character. This case provides a proof of concept for individuating cognitive characters even from an anthropocentric starting point.

2. Distinguishing characters and phenotypes: What and why

The ontology of a phylogenetic psychology is grounded in parts of evolutionary theory that have played little or no role in “evolutionary psychology” and “cognitive ontology” as those research efforts have been pursued.³ Of central importance is the character concept (Wagner 2001).⁴ The terms “character” and “phenotype” are each used in multiple ways in biology, often ambiguous even in context, and sometimes used in combination (e.g., “phenotypic character”). There are correspondingly multiple ways of defining them. The terms are also used in different contrasts:

³ “Evolutionary psychology” focused on explaining *H. sapiens* cognitive phenotypes in terms of their adaptive value for Pleistocene hunter-gatherers (e.g., Tooby and Cosmides 1992; see, e.g., Ereshefsky 2007 for a similar, extended, critique) while those engaged in the current “cognitive ontology” debate (e.g., Anderson 2015; Khalidi 2023) focus on revising our cognitive concepts mainly in the light of the results of fMRI studies of contemporary *H. sapiens* brains and in order to explain *H. sapiens* cognitive phenotypes better. Many have noted the drawbacks for science of this widespread lack of attention to phylogeny across many cognitive fields (e.g., Fitch 2005, 195–96; Rendall and DiFiore 2007, 510; Cisek 2019, 3; MacLean et al. 2012; Finlay and Workman 2013).

⁴ Character identification, individuation, and novelty are research targets in biology at every level of biological organization, from genes to behavior (e.g., Wagner 2001; Platnick 1979; Grant and Kluge 2004; Freudenstein 2005; Wagner and Laublicher 2000; DiFrisco et al. 2020; Love 2007; Brigandt 2003), as well as in classical ethology, whose founders conceptualized behaviors as expressions of behavioral characters (Tinbergen 1963; Burkhardt 2005). That said, discussion has often been filtered through concern with homology (e.g., Hall 2012; Wenzel 1992). “Levels of biological organization” are a useful way of indicating different character schemes developed in different subfields, even though biological reality is not neatly divisible (e.g., Wimsatt 1994).

“Character” is usually contrasted with “character state” in cladistics, while “phenotype” is usually contrasted with “genotype” in biomedical research. I juxtapose them here to highlight a *conceptual* distinction that is basic to sciences of evolved traits and foundational to a phylogenetic psychology.

The concept of a trait—roughly, a property or feature of an organism—can be subdivided into two subtypes. The subtypes correspond to different problems biologists face involving unity and variation in nature. *Characters* are traits individuated across species to capture heritable features that are the same across species despite much interspecies and intraspecies variation. For example, to express the idea that a trait is *highly conserved* in many taxa, the trait must be defined such that it is the same across taxa—that is, as a character. A simple case is the canine tooth character, which can be, and is, shared across humans, narwhals, and other species based on criteria (such as developmental trajectory and position in the jaw) that allow for significant inter- and intraspecies variation. The character acts as a species-neutral standard for determining whether a structure in any species counts as a full-fledged canine tooth, even if it looks and functions very differently across species. Characters (and character states: see fn. 5) typically figure in phylogenetic analyses that enable us to group species by their evolutionary lineages.

Phenotypes are traits individuated within species: They are in the first instance traits unique to individuals, but species-level (or population-level) phenotypes often based on statistical generalizations provide unity within the species to which the individuals belong. Each human’s canine teeth are unique, but we group them into a species-level phenotype—the human canine tooth—that admits of variation within the boundary of species membership. Phenotypes figure prominently in individual differences research, such as how variation in individual (human) susceptibility to tooth decay might relate to differences in their individual (human) genotypes. Characters play little role here because cross-species relationships are not at issue—except of course when we use animal models to make inferences about human phenotypes.

The relation between characters (e.g., the canine tooth) and phenotypes (e.g., the human canine tooth) is best understood as one of determination, where phenotypes are determinates and characters (and character states) are determinables. This is because an individual organism can only belong to one species.⁵ Both characters and phenotypes are “historical” or “etioloical” (or “selected effects”) kinds (Khalidi 2021), although the timescales of their evolution are distinct. And while aspects of a species’ lifestyle and history play a central role in defining and explaining its phenotypes, these considerations may have little role in defining the characters its phenotypes determine.

⁵ The standard example is the relation between being red (determinate) and being colored (determinable) (Wilson 2023). As with other determinates, being one determinate (e.g., a human canine tooth) rules out being another (e.g., a narwhal canine tooth). Mutual exclusivity is also used by some to define character states, or codable conditions of a character, such as “Tail, color: red (0), blue (1)” (from Sereno 2007). However, species membership is also mutually exclusive but is not a condition of a character, and character states are also individuated across species (e.g., two species can have red tails). Thus, character states should not be identified with phenotypes. If a character turns out to be unique to a species, then for any codable condition there will only be one character state of that character, making it contingently coextensive with that aspect of the species-level phenotype.

Finally, the character individuation question addressed in this article is prior to questions about whether two species share the same character, let alone why they may share it—that is, due to common ancestry (homology) or to convergence (homoplasy).⁶ As with their colleagues in biology (see fn. 6), uses of this character concept in psychology are usually couched in discussions of phylogenetic homology (e.g., Matthen 2000; Ereshefsky 2007; Bergeron 2021) but are sometimes explicit (Griffiths 1997, 2006, 2007; Richards 2003; Figdor 2022). However, being shared across species (and thus potentially homologous) is a different issue from being individuated across species. A character might be (a) unique *a posteriori* to one species (a species-level autapomorphy) or (b) shared by two or more species, due to common ancestry (homology) or to convergence (homoplasy). For example, menopause was once thought to be a human autapomorphy but we now know otherwise (for example, killer and pilot whales have menopause). The *a posteriori* nature of this knowledge was possible because menopause was not defined in a way that *a priori* ruled out other species, such as by requiring a human lifespan. As a result, menopause (the character) is no longer classified as a human autapomorphy; the human menopause phenotype is unchanged by this reclassification of the character. It also remains an open question as to whether the character is shared across these species due to common ancestry or not. In short, focusing on homology (how do we determine if a character is shared across species, and, if so, is this due to common ancestry?) is one way to focus on phylogeny. Focusing on character individuation (how do we define a character?) is another.

Beyond here be details that are not critical for my purposes. What matters is that a distinction between cognitive characters and cognitive phenotypes grounds a phylogenetic psychology on the same conceptual basis as that which already grounds biology (making the corresponding label “phylogenetic biology” redundant). This means that to develop a phylogenetic psychology we must use multiple species’ phenotypes to individuate cognitive characters. In contrast, in an anthropocentric psychology, human cognitive phenotypes define the cognitive types, and membership in a cognitive category depends on similarity of nonhuman phenotypes to the human exemplar. Using humans as the reference species for character definition entails that nonhuman cognitive phenotypes will be, at best, less than full-fledged. Of course, legitimate and informative cross-species comparisons are made in anthropocentric psychology. The issue is the basis of the comparisons—how the concepts are defined and category membership determined.

Motivations for revising or replacing our current cognitive types and concepts are legion.⁷ From the phylogenetic perspective, however, traditional cognitive types and concepts need to be revised or replaced because they are typically individuated based on one species’ (i.e., human) phenotypes. Of course, that’s the only possible way to do it if only humans have cognitive abilities. But if other species have them, and cognition evolved, then drawing a character/phenotype distinction in psychology is not optional. To the contrary, it is a well-motivated and appropriate response to

⁶ Biologists use the terms “homoplasy,” “independent evolution,” “convergent evolution,” and “analogy” pretty much interchangeably; these details do not matter here.

⁷ Besides “cognitive ontology” (fn. 3), various calls for conceptual revision come from embodied cognition (Chemero 2009), folk psychology (Hutto and Ratcliffe 2007), empirical psychology (Haidt 2001; Bringmann et al. 2022), and other directions.

recent discoveries of cognitive abilities throughout phylogeny. There are also many other motivations for drawing this distinction:

- (1) It makes possible *a posteriori* claims of uniqueness of a character to a species (or more likely a family, genus, or larger clade).⁸ To say a phenotype is unique to a species is trivial, given how phenotypes are individuated. To say a character is unique to a species is not at all trivial, and presupposes *not* defining the character in terms of one species' phenotype. It is undoubtedly true that humans have many cognitive skills not possessed by their nearest primate relatives (Herrmann et al. 2007). It is also undoubtedly true that humans have many morphological features not possessed by their nearest primate relatives—as long as we are talking about human *phenotypes*. Even if a particular uniqueness claim is about human cognitive phenotypes, it presupposes a conceptual scheme that distinguishes them from cognitive characters—something we do not yet have.
- (2) It is the biological-theoretical justification for the use of animal models for human conditions and features (and vice versa). Translation of results from one species to another is strongest when based on this distinction. The giant squid neuron (specifically, the axon) is an effective model system for nonsquid neurons because we can distinguish what makes it a neuron (character) from what makes it a giant squid neuron (phenotype). We also use human stereopsis as a model system for neural-perceptual links across species (Nityananda and Read 2017, 1) because we distinguish the features that make human stereopsis *human* from those that make human stereopsis *stereopsis*.
- (3) It replaces vague claims of “continuity” and “discontinuity” (e.g., Penn et al. 2008) with the standard evolutionary conceptual repertoire of characters, homology, and related concepts. Similarly, it makes charges of anthropomorphism—the ascription of human-like abilities to nonhumans—a red herring. Phenotypes are both “continuous” (“human-like”) and “discontinuous” (“not human-like”) in different ways. For example, the narwhal's tusk is human-like (because it determines the same character as the human canine) *and* is not human-like (because the phenotype differs). We need not traffic in vagueness and ambiguity if we have the means to express ourselves precisely: A nonhuman species either does or does not have a character that the human species has, and it will never have a human phenotype.
- (4) It enables us to distinguish two aspects to explaining the evolution of human cognitive abilities: explaining the evolution of the cognitive characters our phenotypes determine and explaining the ecological and other pressures of the human lifestyle on the cognitive characters we inherit. While these are complementary research targets, the former foregrounds multispecies comparisons throughout phylogeny (including extinct *Homo* species), while the latter foregrounds the human (*H. sapiens*) species.
- (5) Finally, and most importantly for this article, it entails that research into nonhuman cognition contributes to two distinct (albeit complementary and interdependent) research goals: *Empirical testing for* whether the phenotypes of

⁸ A clade is a monophyletic group comprising an ancestral node species and all and only its descendant species.

a nonhuman species are determinates of a cognitive character and *conceptual testing* of the adequacy of a cognitive character's definition. The focus of this article—cognitive character individuation—falls within this second research goal. The following case studies are cases of conceptual testing that are responses to new empirical findings in nonhuman species.

In noncognitive areas, conceptual testing tends to arise explicitly only when we consider species that are phylogenetically distant from those that have been established to have the character. Given our tradition of cognitive-conceptual anthropocentrism, conceptual testing can arise when we consider cognition in *any* nonhuman species.⁹ These cases raise the crucial issues of identifying those aspects of a human phenotype that do not matter for character definition and those aspects of a nonhuman phenotype that differ from the human phenotype but do not matter for character definition. Resolving these issues is part and parcel of biological individuation—it's temporally extended hard work, not magic. For example, we compare human and narwhal canines in many respects, but we do so having distinguished which features contribute to defining the character (e.g., relative position in jaw) and which do not (e.g., size). Our knowledge of the difference grounds our comparative judgments. As will be shown, perceptual psychology and neuroscience already take this individuation framework for granted. Achieving this conceptual clarity for cognitive concepts and categories is the Holy Grail of phylogenetic psychology.

3. Getting started

How do we move beyond cognitive-conceptual anthropocentrism? A few individual researchers are doing so, albeit without the benefit of a theoretical framework that systematizes their efforts and contextualizes what they are doing and why. For example, Clayton and Russell (2009) suggest a redefinition of the concept of autozoetic consciousness so that corvids are not ruled out *a priori* from having episodic memory (see section 6). Balari and Lorenzo (2015) make an analogous move with respect to the Merge combinatorial operation thought to be a hallmark of language, such that songbirds can also have Merge. A phylogenetic psychology would unify these isolated efforts and prompt more of them. It would also establish a norm of clarifying when the basis for a cross-species comparison is a character and thus a need to attend to how the character is defined. The use of characters in cross-species psychological comparisons should not be left implicit precisely because of psychology's anthropocentric conceptual heritage.

As a first step, identifying and individuating cognitive characters requires having a representative sample of phenotypes that are hypothesized to be determinates of a hypothesized or existing cognitive character and extracting from that sample the features that will define or redefine the character. For example, phylogenetic

⁹ Similarly, Starzak and Gray (2021) argue that the “romantic/killjoy” pendulum endemic to animal cognition debates stem from differences in implicitly held definitions of the abilities being ascribed to animals; Seed et al. (2009) underline the need for detailed knowledge of compared species to isolate relevant differences. Note that conceptual testing is far more empirically and theoretically constrained than “hypothesizing” (Colaço 2022); the case studies will illustrate this.

comparative methods can be extended to psychology to provide an empirically justified framework for choosing which new phenotypes—which new species—might be useful for testing hypotheses of the evolution of a character and its phylogenetic extent (MacLean et al. 2012; Blomberg et al. 2003; Felsenstein 1985). For any given measured trait or set of traits and any phylogeny that relates the initial sample of species, these methods assign a probability that variation in the trait(s) across these species is due to variation in their position in the phylogeny. Behavioral traits, like morphological traits, display this phylogenetic signal, and cognitive characters are likely to do so, along with social and cultural characters implicated in sociocultural explanations of the evolution of cognition (e.g., Holekamp 2007; Whiten 2021; Boyd et al. 2013; Mace and Holden 2005). Notably, phylogenetic signal will be very low or nonexistent if the sample includes phylogenetically very distant species because in this case phylogenetic position makes little difference to whether a species has the trait.

We can also examine proposals for conceptual revision to reveal how the addition of new phenotypes (new species) impacts character individuation decisions. Epistemically, researchers offering revisions can make explicit what may be implicit in standard definitions, forefront key new evidence relevant to individuation, show how different types of evidence and features are weighed, and justify that revision as opposed to alternatives. Metaphysically, revisions show how features of the phenotypes of a new species affect the way the character is defined. They classify observed features of at least one new species' phenotype as allowable variations of the character rather than reasons for excluding it as a determinate of the character. This can also further our understanding of how a character evolved if the revision eliminates an explicit or implicit criterion that had restricted it to clades to which the new species does not belong (e.g., the nervous system case in the following text). What we know about the newly included species' clades also becomes relevant to hypothesizing the character's origin and phylogenetic extent.

Proposed revisions of the stereopsis and nervous system characters (sections 4 and 5) are highly informative in these respects. In these cases, the problem of initial character identification has been resolved. But character revisions exist in a normative penumbra between the way we ought to define a character and the way we do. All proposals to revise current cognitive types are in a similar penumbra with respect to human cognitive phenotypes. If we accept that cognition evolved, then we ought to define cognitive types that are not *a priori* uniquely human—cognitive characters. Proposed revision of the definition of episodic memory (section 6) shows how we can leave cognitive-conceptual anthropocentrism behind. We can then define uniquely human cognitive phenotypes based on this nonanthropocentric conceptual foundation.

4. Stereopsis and the praying mantis: Acceptance and integration

The common shorthand definition of stereopsis is depth from disparity—the ability to extract depth information from disparity in the visual input into two eyes. It was first experimentally shown in humans (Wheatstone 1838) and was long thought to be uniquely human. Only much later it was demonstrated in the first nonhuman species (macaques) (Bough 1970) and in praying mantises fairly recently (Rossel 1983). Stereopsis has been experimentally shown in many other species since, ruling out an initial hypothesis that, even if not uniquely human, it was limited to mammals and (of

course) most advanced in primates. However, the main competing hypothesis—that any species with binocular vision has stereopsis—also seems false, given that chameleons don't demonstrate it. So, while we do know it is widespread we don't know its phylogenetic extent. Moreover, the disentangling of stereopsis from binocularity suggests that stereopsis confers its own adaptive advantages, and that different species with stereopsis can differ with respect to the selective advantages stereopsis provides to them. If so, we might suspect that stereopsis can be found in different forms (phenotypes), just as canine teeth have evolved into different forms.

I have just demonstrated character-thinking about stereopsis. That's not the only way to think about it. For at least some psychologists, stereopsis essentially includes an experience of depth—the visual experience humans have when we perceive depth. There is no one right definition here except in the following key sense: In cross-species comparisons of stereopsis, we need to be clear whether the compared features are ones we think define the human phenotype or else define the character. If the features defining the human phenotype just are the features defining the character, we are doing anthropocentric comparative psychology. If we separate them, we can say both that human stereopsis essentially includes an experience of depth (the experience partly defines the phenotype) and that praying mantises have true stereopsis even if the experience of depth is unique to humans (the experience doesn't partly define the character). What we must avoid doing is building a feature associated with the human phenotype into the definition of a character—not unless we define that feature as a character.

Rossel's (op. cit.) work prompted further empirical testing for stereopsis in a greater range of nonhuman species and for further details of praying mantis stereopsis. In the light of these accumulated results, Nityananda and Read (2017; Nityananda et al. 2018; Read 2023; henceforth N&R) initiate conceptual testing by proposing to revise the definition of stereopsis in targeted ways. Their revision reveals the metaphysical impact of including the praying mantis stereopsis phenotype as a determinate of the stereopsis character. Note that it is assumed that praying mantises have stereopsis and that they have it by convergence. The question here is: How do the differences in the way praying mantises exhibit stereopsis motivate researchers to redefine the stereopsis character?

On their view, stereopsis is “the ability to gain information about the 3D structure of visual scenes by comparing information collected separately and simultaneously from different lines of sight to the same region of space” (N&R 2017, 2504). The simplest revision here is the relaxation of a requirement for binocularity. Not all expressed stereopsis definitions state a binocularity requirement explicitly, although binocularity is treated as a criterion in practice. This it-is-and-it-isn't criterial status likely reflects a lack of interest in definitions once researchers can state a generalization that covers all or nearly all current targets of research. The criteria of such definitions, stated or not, are best thought of as revisably necessary—they rule out cases (as criteria should), but we are always open in principle to changing our minds, especially in the light of new evidence.¹⁰ In these terms,

¹⁰ In Feest's (2017) terms, stereopsis would be a phenomenon, not an “epistemically blurry” object of research, but even definitions of phenomena remain revisable as we learn more about them. In Feest's terms, cognitive characters would be objects of research.

binocularity was a revisably necessary criterion of stereopsis since 1838, and N&R's 2017 revision suggests that two lines of sight, rather than two eyes, is the appropriate revisably necessary criterion instead.

The other major change is the relaxation of the criterion of obtaining depth information specifically. Researchers had assumed stereopsis depends on static disparities between the two images and that its main purpose was distance estimation, adding detecting object boundaries (or breaking camouflage) later on (Julesz 1971). Human stereopsis systems use static disparities between images and can estimate distance and break camouflage for motionless targets, although we are pretty lousy at estimating distance just using stereopsis. The praying mantis uses kinetic disparity (motion and changes in luminance) between retinal images to estimate distance. If prey-like stimuli are not moving and are perfectly monocularly camouflaged, this form of stereopsis is unable to break the camouflage to see the target's boundaries. This suggests that the relations between computing depth (specifically), estimating distance, and detecting boundaries are more complicated than we had thought. In particular, it is not known if the end uses of stereoptically derived information—estimating distance and detecting object boundaries—depend on computing depth, or if 3D information obtained from the visual input can be used directly for these independent functions without going through a computation of depth. The revision to obtaining 3D information is intended to leave open exactly how these functions are related.

Why these revisions? The praying mantis is an invertebrate ambush predator with compound eyes. Functionally, its form of stereopsis suffices for estimating distance to moving prey, but potentially not for detecting boundaries of static camouflaged objects. Structurally, it is in the same major clade as mantis shrimp, another invertebrate group that can obtain multiple lines of sight from one of its compound eyes (Schiff et al. 1985). Its phylogenetic position has also prompted research into stereopsis in other invertebrates, such as cuttlefish (Feord et al. 2020).

The stereopsis example introduces two important methodological principles in character individuation, which will be reinforced by the case of the nervous system discussed in section 5.

1. Phenotype Inclusion. Are the phenotypes that might newly count as determinates of the character *prima facie* acceptable in the light of phylogeny? In the best of circumstances, a revision proposal initiates a process in which the relevant research communities consider the revision as research continues. In this case, praying mantis stereopsis has been accepted for decades, though details of its stereoptic system were not known. This *prima facie* acceptance of its behavior as sufficient evidence to infer to stereopsis was essential for its visual system to be a target of additional stereopsis research. Epistemically, the range of phenotypes that count as evidence of the character has expanded. The potential metaphysical consequence is character redefinition based on features of a new species' phenotype and its phylogenetic position.

This process is iterative: (1) a character is initially defined based on a few species' phenotypes; (2) a new species is empirically tested for presence of the character and, depending on the results, its phenotypes are *prima facie* accepted as determinates of it by a sufficient number of researchers in the relevant fields; (3) further investigation of the new phenotypes reveals features that suggest revision of the character;

(4) a proposed character redefinition is offered; (5) a new species is tested; and so on, until we reach a stable (if always revisable) consensus on the character's definition and phylogenetic extent.¹¹ This is why the choice of species in a comparative study is metaphysically crucial: The phenotypes of the species in the sample are *prima facie* accepted as determinates of the characters being compared. For example, when using phylogenetic comparative methods (e.g., MacLean et al. op. cit.) it is implied that the variables, which represent characters, are defined at a particular taxonomic level—for example, primates, or mammals, or vertebrates, or whatever, depending on the sample. If the sample includes phylogenetically very distant species, the characters (variables) must be very broadly defined indeed.

Prima facie acceptance may or may not amount to belief in truth. But, first, few will waste time and money on additional research without having sufficiently high credence in the proposition (e.g., that the praying mantis has stereopsis). Empirical research has multiple significant opportunity costs. Second, a research community can effectively block empirical and conceptual progress if it dismisses a species from the outset as not having the character, on whatever grounds. N&R could not have initiated conceptual testing of the stereopsis character if initial praying mantis results had been dismissed within the relevant research community. Among stereopsis researchers, those pushing back on their redefinition—“That’s not true stereopsis”—have largely been psychologists who hold an “experience of depth” definition associated with human stereopsis (VN/JR, personal communication). It may not be clear whether the experience of depth is being cited as a criterion of the human stereopsis phenotype or of the stereopsis character. If the former, no harm done: Praying mantises don’t have human stereopsis. But the silent merger of these two claims—in which only human stereopsis is true stereopsis because it alone (so far as we know) satisfies the experience criterion—yields perceptual-conceptual anthropocentrism.

Finally, *prima facie* acceptance falls within normal standards of scientific rigor, which involves undertaking replications, finding confounds in published research, and so forth. A new species’ phylogenetic position is always a factor. Finding stereopsis in a previously untested mammal would not raise any eyebrows; finding stereopsis in an invertebrate remains of note, though acceptance for one can promote acceptance in others; finding stereopsis in a bacterium is very unlikely to be accepted (but can’t be ruled out *a priori*).¹² *Prima facie* acceptance for cognitive abilities is exceptionally difficult because *every* nonhuman species raises eyebrows given our anthropocentric history, and ordinary scientific skepticism can be turbocharged by invocations of Morgan’s Canon and claims of “anthropomorphism.” These charges enable elision of the two goals of comparative research mentioned previously—

¹¹ This may be regarded as an instance of what Chang (2004) articulates as a process of “epistemic iteration,” here in the context of cognitive character individuation.

¹² Whether the two lines of sight must be in an eye may (in the future) be revised. A cyanobacterium (genus *Synechocystis*) uses its whole cell as a lens and the surrounding membrane, which contains photoreceptor proteins, as a retina to achieve low-resolution and imaging, even though it does not have eyes or photoreceptor cells (Nilsson and Colley 2016; Nilsson 2013; Nilsson and Pelger 1994). Accepting *Synechocystis* as perhaps the “smallest and oldest example of biological cells serving as bio-microlens on earth” (Pan et al. 2021), if two lenses of one eye can perform stereopsis, we might speculate that two bio-microlenses might suffice, even if no single *Synechocystis* bacterium can do it (but maybe two acting together can).

empirical testing of whether a new species has a character and conceptual testing of the adequacy of the character's definition.

2. Character Integration. What characters are included in the target character? Some characters may be simple in that they only have one criterion. However, in many cases there will be multiple criteria, including cases in which structural and functional characters will be integrated (and weighed).¹³ The stereopsis revision to require two lines of sight replaces one structural requirement (binocularity) for another (at least one eye, as long as it has multiple lines of sight). This is not an “operational definition” in the sense of defining a construct in terms of a test or probe, as one might define hardness in part by a scratch test. The tests for the presence of binocularity were not in the definition; binocularity was in the definition, and the evolved behavior we test depends on the evolved body that is behaving. These structural components of functional definitions are in principle always revisable even if the function is not revised—for example, if N&R had suggested only the monocular revision. That is the methodological upshot of multiple realizability. But the structural components that are already there provide plenty of *a posteriori* ways to exclude new phenotypes from being considered determinates of a given character.

I will elaborate further on this principle after discussing the nervous system case in the next section. However, it is worth noting that character integration implies that putatively purely functional cognitive characters are literally of no use in empirical science until they are structurally defined in part. Some may prefer to hermetically isolate structural criteria into operational corollaries that enable the use of purely functional characters in empirical research, where observable evidence is mandatory. But this position mischaracterizes the determination relation between the character and the phenotype—all the behaviors we test are done by bodies, and the ways these bodies perform the behaviors fall within the physical restrictions on what counts as a determinate of a component structural character. In psychology, we know many behavioral characters are “not easily connected to structural underpinnings” (Rendall and DiFiore 2007, 507), whether these are defined fairly narrowly (e.g., burying feces, food storing, nest building, song learning) or very broadly (e.g., range use, female exogamy, polygynous mating, conflict resolution) (Rendall and DiFiore *op. cit.*; Duda and Zrzavý 2013; Thierry et al. 2008; DiFiore and Rendall 1994). But a lack of any connection is tantamount to declaring that behavior did not evolve (Rendall and DiFiore 2007, 505). Bodies, behavior, and cognition all evolved together; the use of physical proxies to investigate the evolution of cognition (Dediu and Levinson 2013; Currie 2018) relies on this fact.

5. The nervous system and plants: Autonomy and hierarchy

Prima facie acceptance of stereopsis in the praying mantis in 1983 did not usher in immediate metaphysical consequences; the accumulation of research prompting proposed concept revision took several more decades to obtain. The case of the

¹³ The contrast here is with traditional functionalism in philosophy of mind and cognitive science, where functional definitions lack physical components (e.g., Putnam 1975): Character integration implies that morphology might constrain cognition using morphological criteria of cognitive character definitions. For space reasons, I must set aside full discussion of this implied rejection of the principle of medium independence for another opportunity (but see also section 5).

nervous system character is similar. Bose (1926) showed that plants have long-distance cell-to-cell signaling systems and proposed revising the nervous system and neuron characters to include plant phenotypes as determinates of these characters. His proposal had little uptake at the time (Minorsky 2021), and plant phenotypes are still not widely accepted as determinates of these characters, despite further research on plant signaling and calls for plant neurobiology (Trewavas 2003; Brenner et al. 2006). Miguel-Tome and Llinas (2021; henceforth MT&L) are revisiting the issue.

MT&L propose to redefine the nervous system character by eliminating neurons (a.k.a. nerve cells) as necessary components of nervous systems. Their full definition is that a nervous system is “a system of a multicellular organism that (1) contains a group or groups of cells that are specialized in transmitting, generating, or processing information; (2) sends signals to other systems, allowing the organism to react to or act upon exogenous or endogenous states by controlling those systems’ activity, and (3) generates and sends signals to other systems as the result of communication among multiple specialized cells of the system.”¹⁴ The action-potential-based functioning of a nervous system is the same, while the cell types that perform it can differ. In their terms, their redefinition is not “phylogenetic” because it eliminates reference to the animal kingdom, given that all and only animals (except sponges) have neurons by current definitions. It also splits the difference between Bose and (e.g.) Brenner et al.: MT&L deny plants have neurons but agree that talk of plant neurobiology is “reasonable” (7) if it is talk of plant nervous systems. In this case, it is given that plants have internal signaling networks, and the question is: How do the known differences in plant signaling affect how we define the nervous system character? For many, they have no effect; MT&L disagree. But if plants do have nervous systems, they are homoplasous in relation to animal nervous systems.

This redefinition affirms the importance of action potentials, neurotransmitter molecules, and specialized multicellularity: Signaling within or between bacteria is excluded, and a nervous system must still be made up of specialized cells (Bullock et al. 2005). By challenging just the idea that neurons are necessary, the redefined character is “general enough to allow discussing convergent and divergent evolutionary processes but not so general that it becomes meaningless by including any system of signals.” (MT&L op.cit.: 1) In addition, molecular-level homologies in plant and animal signaling systems—for example, the same signaling molecules GABA and glutamate, though perhaps not with the same functional roles—are among the empirical discoveries that prompt their revision. They do not embrace homology of plant and animal nervous systems. This would entail the implausible hypothesis that the last common ancestor of plants and animals (thought to be very simple) had a nervous system or its ancestral character.

MT&L also consider how a nested hierarchy of nervous system characters might be developed, just as many other characters are (Platnick 1979). A nervous system is a specific type of a command-control system in a multicellular organism; the command-control category includes hormonal systems or any other biological subsystem that generates, transmits, or processes information. They suggest defining a hierarchy of increasingly more specific nervous system characters within the

¹⁴ Shortened (p. 8): A species’ internal signaling system is a nervous system if it “transmits, processes, and generates cell-to-cell action potentials, with specific types of uptake.”

biological realm by integrating increasingly more specific physiological and anatomical criteria into the definition.

Research based on their proposal shows its effective fruitfulness. Broadening the neuron character to include plant cells would have entailed that having synapses is not a significant enough difference to matter in many research contexts. When coding different species' characters for phylogenetic analysis (e.g., assigning 1 for presence of neurons, 0 otherwise), the plant and animal cells would be coded the same. This would have risked obscuring important research questions based on distinguishing neuron-versus nonneuron-based nervous systems.¹⁵ For example, Moroz and Romanova (2021) have investigated the specific adaptive benefit(s) to an animal of having gaps (synapses) between the cells in its nervous system, beyond the general adaptive benefit(s) of cell-to-cell signaling. We might also ask whether synapses are needed for associative learning, given inconclusive results of associative learning in plants (Gagliano et al. 2016; Loy et al. 2021), and what specific adaptive benefits(s) synapse-less nervous systems confer. Research on these and other questions can in turn provide insight into our understanding of the evolution of neurons, brains, and brain-based animal cognition, as well as plant learning and potentially plant cognition.

This proposal adds further complexity to character relationships and introduces the idea of defining characters in a nested fashion:

3. Constrained autonomy. How are characters at other levels of biological organization weighed in an individuation decision? Phylogeny taxonomizes species, but there are multiple character taxonomies—for example, genetic, molecular, developmental, morphological, behavioral—at different levels and sublevels of biological organization. Levels divisions affect character individuation when a character within a definition is individuated at a different level or sublevel from the one being defined. Some characters may be individuated without taking characters at other levels into account (just as they may not have multiple components or criteria). But for many traits, including cognitive traits, features at different levels will play a role.

At the same time, character individuation is significantly autonomous at any given level (as is homology: Ereshefsky 2012). For example, homologous homeobox genes in all eukaryotes direct the development of nonhomologous eukaryote body plans. In this case, MT&L's revision entails that nervous systems in plants and animals (1) contain homologous signaling molecules (same character, inherited from the last common ancestor), (2) are composed of distinct cell characters (different characters), and (3) determine the same nervous system character (same character, independently evolved in each kingdom). Given the same large phylogenetic distances, individuation of functional and structural components and the hypothesized phylogenetic relationships differ. In a phylogenetic framework, the theoretical concern for psychology and philosophers of psychology will be how to understand the autonomy

¹⁵ In other terms, lumping versus splitting choices must take phylogenetic position into account: lumping two *phylogenetically distant* species' phenotypes together as determinates of the same character can make phylogenetic comparative methods much less (or un-) informative and make useful distinctions invisible (e.g., Pellis 1988; Rendall and DiFiore op. cit., 510). Advocates of ascribing cognitive abilities throughout phylogeny (e.g., Lyon et al. 2021) may see this as a feature; those trying to trace the evolution of cognition are likely to consider it a bug.

of psychological characters in the light of similar functional, structural and phylogenetic complexity.

4. Nested hierarchy. How can characters be individuated more finely (/broadly) as clades get smaller (/larger)? MT&L sketch a hierarchy of signaling system types of the sort that characterizes other characters, whereby smaller clades have the characters that define the larger clades they are in, plus some additional character or characters (Lauder 1994). In morphology such character hierarchies are well established. The general pattern is one in which characters differentiate in the course of evolution, just as speciation results in distinct clades and species from a common ancestor. For example, some characters, such as DNA, are found in just about all extant organisms; others, such as homeobox genes, are very widely distributed (all eukaryotes, no prokaryotes); many, such as having vertebrae, are more limited in phylogenetic extent. A nested hierarchy of cognitive characters will also depend on the degree to which behavioral characters can be nested (see also Griffiths 2006, 5). Distinctions in learning types indicate how this might go. If only some organisms that habituate are capable of associative conditioning, and only some of those capable of associative conditioning can learn by unlimited associative conditioning, then plausibly there is a nested hierarchy of cognitive abilities required for these types of learning, only some of which may be restricted to the animal kingdom (Carrasco-Pujante et al. 2021; Ginsburg and Jablonka 2019).

As noted, MT&L's sketch of how to obtain increasingly more specific nervous system characters in a nested hierarchy entails character integration. From a phylogenetic perspective, structural criteria are a boon to understanding cognition because they promise to help us define cognitive characters at the multiple levels of *phylogenetic* grain that we need. We can define very broad behavioral characters (such as in biocybernetic terms of feedback-control loops) but such characters are useless for making many of the cognitive inferences we want to make in psychology—the behavior may be cognitively controlled in one species but not another, and even if we assume it is always cognitively controlled the means of control in one species may differ importantly from the means in another. In addition, behavioral traits seem to evolve further than some of the underlying morphological and physiological traits—for example, developing a novel diving ability without developing more specialized morphology or physiology that would facilitate diving (Blomberg et al. 2003). Inferences to novel cognitive characters may be more reliable if they are made from more fine-grained behavioral characters that include structural criteria. Otherwise, we hobble ourselves unnecessarily in any effort to distinguish, say, an ancestral decision-making character found in bacteria and primates, and a derived decision-making character found only in primates. The usefulness of phylogenetic comparative methods in psychology depends in part on our having at least a rudimentary behavioral and cognitive character hierarchy of this sort.

6. A speculative cognitive example: Episodic memory in scrub jays

The preceding two cases show how empirical results in new species motivate targeted revisions of character definitions. An equally clear example of redefinition of cognitive abilities is more challenging: Any redefinition to transform a concept based on a human cognitive phenotype into one that picks out a cognitive character can

invite the response that the revised concept doesn't pick out the real thing. But we can still consider how such redefinition might go, using the case of episodic memory. The question here is: How do we get to cognitive characters at all? How do we define cognitive abilities nonanthropocentrically, so that nonhumans are not ruled out *a priori* from having them? This case is conditional on accepting for the sake of argument that episodic memory is a natural kind (distinct from semantic memory) and that we have sufficient evidence of conscious experience in at least some nonhuman animals. But the benefit is that it provides a cognitive proof of concept.

Tulving (1972) originally defined episodic memory in terms of storing and retrieving information about temporally dated events and temporal-spatial relations among events. Using this definition, Clayton and Dickinson (1998) designed experiments that took advantage of scrub jays' natural behavior of caching food items for future consumption. These included wax worms, which are preferred but also spoil quickly, and peanuts. By manipulating the period between when the birds cached the items and when they could be retrieved, they found that the jays would retrieve the wax worms if the period was small but would skip them and retrieve the peanuts after the longer periods. In short, the birds showed recall of what, where, and when they cached the different items.

Skeptics (e.g., Suddendorf and Corballis 2007) objected that this did not show that they were reexperiencing having cached the food items, and Tulving (2005) updated his definition to add that true episodic memory requires mental time travel (MTT) or auto-noetic consciousness: A reexperiencing of the past event that has a conceptualized experience of the self as part of its content. As Clayton and Russell (2009) note, while the jays' behavior would have justified inferring to true episodic memory under Tulving's original definition, the later definition puts it out of reach. So "if we are serious about the very possibility of [episodic memory] existing in animals" (2009, 2331), a theoretical response is required.

One such response is to reject the new reexperiencing criterion (Allen and Fortin 2013). Clayton and Russell (2009) accept it, but make episodic memory possible for nonhumans by distinguishing the adult human reexperiencing phenotype (MTT) from a reexperiencing character. Their proposal draws on Kantian ideas of *a priori* and nonconceptual intuitions of space and time as conditions for all experience (e.g., Hanna 2008). The reexperiencing character requires a perceptual, nonconceptual perspective in relation to the recalled event—for example, reexperiencing the spatial viewpoint toward an object that was experienced in the original episode. This character would be determined by nonhuman and human infant reexperiencing phenotypes as well as the human adult phenotype. As they put it (op. cit.: 2331), "[J]ust as human episodic memory will inherit what was present in human experience, avian episodic memory will inherit the character of avian experience" (where "character" here is the sense of "characteristic"). The two species' episodic memory abilities would be unique as phenotypes, but they would determine the same episodic memory character. Clayton and Russell don't also consider the follow-up question of *why* they may share the same character—that is, the question of homology. Their concern is individuating a cognitive character. In any case, it's likely that human and avian episodic memory would be related by convergence, not common ancestry.

Whether or not their proposal ends up being accepted, it represents a substantive theoretical advance in terms of conceptualizing episodic memory phylogenetically. Humans might still have the episodic memory character uniquely (a species-level autapomorphy), but this would be an *a posteriori* matter. Alternatively, some nonhuman animals might also have episodic memory, not something merely episodic-memory-like. These are unambiguous, and unambiguously empirical, alternatives once a cognitive character/phenotype distinction is in place.

7. Conclusion

Progress in psychology as an evolutionary science requires thinking of human cognitive abilities as determinates of cognitive characters. This means adopting the working hypothesis that the characters our cognitive phenotypes determine are not unique. Only by making this defeasible assumption can we tease apart the contributions to our current phenotypes of (1) evolutionary inheritance starting from when a cognitive character first appeared in phylogeny; (2) within-lineage evolutionary developments in a character from when *Homo* species first appeared; and (3) relatively contemporary adaptive pressures on *H. sapiens*. *H. sapiens* may have a novel cognitive character or character state, or only nonunique characters; it may have a novel combination of nonunique characters; or what is novel about us is not a character-level distinction at all, but simply a remarkable phenotype (like the narwhal's tusk). All these ways of affirming human cognitive uniqueness require a character/phenotype distinction.

This article has motivated clear areas of research needed to develop a phylogenetic psychology. How can we leverage structure to define more fine-grained behavioral and cognitive characters, both those nested in the phylogenetic hierarchy of clades, and potentially those defined at different biological levels within an organism? How do we develop a conceptual and linguistic scheme that will enable us to avoid ambiguity when referring to cognitive abilities across species, at different levels of phylogenetic generality, and within organisms at different levels of biological organization? Philosophers of psychology are well-positioned to offer the metaphysical and linguistic/conceptual expertise required to answer these and other pressing questions for putting psychology on a firm phylogenetic footing.

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