# What Could Cognition Be, If Not Human Cognition?: Individuating Cognitive Abilities In the Light of Evolution<sup>1</sup>

#### **Carrie Figdor**

## (forthcoming (relative to September 2022) in *Biology & Philosophy*)

## 1. Introduction

This paper argues for the individuation of cognitive abilities within cognitive sciences based on the same phylogenetic framework that underlies the individuation of parts and traits at multiple levels of biological organization in comparative biology. When our scientific interests directly involve cross-species comparisons, this is the operative framework. When they do not, the units we are interested in, as explananda or explanantia, presuppose this comparative framework.

The need for explicit adoption of this framework stems from two broad sources in recent cognitive research. One source is the discovery or posited existence of cognitive abilities in biological entities not at all similar to humans, such as bacteria and plants, as well as to a wider range of familiar entities, such as birds, insects, and octopi. This expansion remains contested in no small part because it is not clear what abilities are being ascribed when familiar psychological terms are used to ascribe them (e.g. Figdor 2018). The other source is research that aims to explain

<sup>&</sup>lt;sup>1</sup> I wish to thank Paul Griffiths above all for a year of fruitful interactions with him and those in his Theory and Method in Biosciences research group (especially Pierrick Bourrat, Stefan Gawronski, Kate Lynch, Peter Takacs, Joshua Christie, Elena Walsh, Axel Constant, and Wesley Fang) during an Anderson Fellowship research visit at the University of Sydney in 2019. This paper and those to follow are consequences of the fellowship. Paul, Stephen Downes, and Matthew Sims all provided helpful comments on one or another draft, and Paul and Peter provided many helpful suggestions for additional research. I was also helped greatly by questions from audiences at the many institutions where I gave talks (many online) based on the then-current draft in 2020 and 2021: University of Edinburgh, Kings College London, University of Sussex, University of Groningen, University of Iowa, TU-Berlin, University of Warwick, University of Sheffield, and the Max Planck School of Cognition. Finally, I thank an anonymous reviewer for this journal for comments that prompted important clarifications in the penultimate draft.

the evolution of human cognition. This research often involves claims about the ways in which human cognition is unique. But uniqueness is a comparative term, and such claims are often ambiguous as to whether the explanandum human ability is being individuated in the way that comparative claims require.

In both cases we need a framework within which we can ask the difficult questions of what what counts as the same evolved cognitive ability and what does not. This paper articulates that framework in terms of two simple principles that guide individuation in evolutionary biology, and comparative biology in particular. In metaphysics-of-science terms, they tell us what it means to accept characters into one's ontology. Explicit integration of cognitive characters in the cognitive sciences would enable us to shift our criteria for individuating cognitive abilities from similarity to humans to the evolutionary constraints that apply to all evolved traits. Some researchers are already embracing this framework, as illustrated below. But making it explicit would promote making it as necessary to psychology as it is to biology.

I introduce the character concept in evolutionary biology and elaborate its basic explanatory role in Section 2. I will explain what characters are, what commitment to them amounts to, and the theoretical, explanatory, and methodological differences such a commitment would make. In particular, it exposes unjustified presuppositions about human cognitive uniqueness that can linger even after embracing evolution, and it clarifies how evolution constrains ascriptions of cognitive abilities across species.

I expand on the implications of embracing characters in cognitive science in the following sections. I discuss the implications for debates about the relation between human and nonhuman cognition (the "continuity/discontinuity" debate) in Section 3 and about the extent of biological cognition (the "what is cognition?" debate) in Section 4. These debates represent two approaches

2

to the same problem: how should cross-species comparisons of cognitive abilities be made if they are made in the light of evolution, where "in the light of evolution" is in the light of descent with modification, not in the light of adaptation (Dobzhansky 1973; Griffiths 2009)? I provide examples of how some cognitive scientists are introducing characters into their explanations of "high-level" cognitive abilities, and how others would clarify their hypotheses if they did. I use research on episodic memory, language, and sociocultural origins of cognition in Section 3, and the basal cognition approach in Section 4. These examples show the pressing need in cognitive science for phylogenetic concerns to ground cross-species comparisons of cognitive abilities. The conceptual innovation required would help meet what Heyes (2013: R100) calls an "urgent need to find the right kind of evolutionary thinking, and the right place for it, in psychology", and in any other field or subfield investigating cognition in biological organisms. I will usually use "cognitive science" as an umbrella term for all these fields, but only because "psychology" is associated with humans (except when modified with "comparative").

As a final introductory note, the issue addressed here of integrating characters into cognitive science is distinct from more familiar ways in which biological and cognitive theorizing interact. First, the specific research programme of Evolutionary Psychology (e.g. Barkow, Cosmides, and Tooby 1992), with its focus on natural selection, seeks to explain how human psychological, particularly cognitive, abilities evolved using adaptationist hypotheses. My concern is how phylogenetic concerns constrain the way cognitive abilities must be individuated. This difference can be put in terms of two of Tinbergen's (1963) four questions regarding a biological explanation of behavior (discussed further below): Evolutionary Psychology focuses on the question of survival value, whereas my concern is the question of phylogeny. Both questions are

"evolutionary", but they are different questions.<sup>2</sup> Second, naturalistic theories of mental content advert to biological functions – in particular, selected effects – to explain mental content or intentionality (e.g. Millikan 1984, Neander 2014). My concern instead is cognitive ability types and the distinction between characters and phenotypes (explained below). Their project is essentially adaptationist and non-comparative; mine is essentially comparative and not essentially adaptationist. Third, biological knowledge also informs debates in mind-body metaphysics and the metaphysics of biology (Piccinini 2020; Dupre 2021; Bueno, Chen, and Fagan 2018). My concern is the ontological commitments of phylogenetic evolutionary explanations. One can embrace physicalism without quantifying over the types of entities these explanations require.

### 2. What is a character?

The central explanatory principle of the theory of evolution is descent with modification via natural processes. The primary explanandum has been speciation, displayed in branching phylogenies of extinct and extant species related by ancestry. However, the features, parts, or traits of organisms at all levels of biological organization – e.g., genes, gene regulatory networks, developmental pathways, morphological structures, behavior – also evolve. The evolutionary trajectories of these entities are captured in the character concept. Both species and characters, along with the evolutionary relationships between species and the identification of characters across species, are key explananda and explanantia in the continuities and discontinuities that comprise the process of evolving life.

<sup>&</sup>lt;sup>2</sup> See also Vonk and Shackelford (2012) on the distinction between evolutionary psychology as the specific research programme and evolutionary psychology (what they call comparative evolutionary psychology) as the study of psychology, human or otherwise, under the unifying framework of evolution. This paper falls within, and contributes to, the latter.

As will become clear below, the distinctive significance of embracing the character concept in cognitive science stems from a specific way in which it rules out the pre-evolutionary metaphysics of the Scala Naturae (or Great Chain of Being). In the latter, species were individuated and sharply distinguished by their distinct, unchanging essences, and were arranged in a linear order by their degree of perfection relative to that of the Abrahamic God (Lovejoy 1936). Human cognitive uniqueness was necessitated by the nature of the human essence as reason, or nous in its Aristotelian origin. By rejecting traditional essences and sharp boundaries between species based on them, evolution entailed that the timescales of transformation and periods of stability of species and of whatever traits took the place of essences would at best yield contingently aligned boundaries between them. In other words, evolutionary theory ruled out the necessary connection between the human species boundary and the boundary of cognition. It made the link between being human and having "high-level" cognitive abilities (i.e. high on the Scala Naturae) metaphysically insignificant. This contingent connection is not limited to the human species and cognitive traits. It is constitutive of the character concept. But because of the influential Western intellectual heritage articulated by Lovejoy (op.cit.), the change has particular resonance in cognitive science.

The original character concept was introduced by Owen in order to explain anatomical stability across species boundaries that could not be explained by the sameness of function across species (Owen 1849; Hall 1994).<sup>3</sup> In Owen's definition – "the same organ in different animals

<sup>&</sup>lt;sup>3</sup> Darwin proposed a similar distinction between "Unity of Type" and "Conditions of Existence"; see Griffiths 2007 and Erwin 2021 on historical views related to contemporary character concepts. The ontology of characters is still a matter of debate, akin to the well-known species problem and related to the problem of understanding when two phenotypes in different species express the same character (see, e.g., Platnick 1979; Colless 1985; Hall 1994; Lauder 1994; Grant and Kluge 2004, Freudenstein 2005, Laublicher and Wagner 2000, Wagner 2001, 2014). Homology too has been defined in distinct ways (Ereshefsky 2012 provides a concise summary). While homology is not

under every variety of form and function" – the "same organ" is the character that the anatomical phenotypes of different species express. Whether they are similar in adaptive function is not criterial for sameness of organ. Some definitions of the character concept continue to identify it with structural parts of organisms. But broader definitions capture the concept as it is used today in many posited phylogenetic or historical homologies – that is, in posited lineages of identical characters across at least two species due to their common ancestry. Characters need not be homologous, but there are no homologies without characters.

In contemporary usage, a character is a unit that encapsulates the evolutionary-historical constraints on phenotypic development and expression. Characters help explain why evolution is not fully random. For example, specific patterns of digit loss in phylogeny are characteristic of current urodele (salamander) limb and anuran (frog) limb phenotypes respectively. The urodele limb and the eu-tetrapod limb are the characters that capture these historical guardrails on the distinct ways in which the limb phenotypes of the organisms within each group develop today (Wagner 2014). These constraints on the variation and variability (or variational tendencies) of phenotypes include interdependencies between characters and reservoirs of variability that may

of central concern here, my references to homology are to phylogenetic or historical homology, which involves identical characters in two or more species that have a common evolutionary origin (usually relative to the species' most recent common ancestor). There is also general agreement that a character can take on alternative forms called character states, akin to the alleles of a gene – e.g., the hind wing character of insects has wing blade and altere character states (see Duda and Zrzavy 2013: 427-428 for a sample table of characters and character states). Despite these unsettled conceptual issues, biologists agree on many examples of characters, character states, and homology, have ample empirical motivation and evidence for positing characters, and consider them critical targets of and elements in evolutionary explanations. For my goal of showing the importance of the character concept for explaining cognition, it suffices to explain its explanatory role and to highlight the key features that define commitment to characters. I set aside (as not critical here) serial homology (character repetition within an organism, e.g. cervical vertebrae) and homoplasy (variously defined as non-homology, analogy, or as the opposite end of a spectrum of similarity from homology, e.g. Boyden 1947, Ghiselin 1976, Hall 2005).

only become available to natural selection in new environmental contingencies (Moczek 2008; Shettleworth 1993, 2012).

Characters are also critical for distinguishing real from superficial trait similarity by reference to evolutionary history. Historical sources of stability interact with adaptive pressures to make it possible for every combination of similarity relations between phenotypes that express the same or different characters to occur. What strikes us as similar is not a reliable indicator of sameness of character, and many highly adaptively significant phenotypic variations have no impact on character individuation. A human left upper canine tooth expresses the same canine tooth character as the tusk of an adult narwhal (typically male). Similarly, the presence or absence of webbing between digits is highly adaptively significant for a species, but irrelevant for individuating the tetrapod digit character (Hall 2003).

Individuating characters, identifying homologies and their various empirical grounds, and identifying character novelty are significant challenges at any level of biological organization.<sup>4</sup> These challenges represent enormous areas for cognitive scientific research – once the character concept has been embraced. To motivate that embrace, I isolate the key features of the character concept in two basic principles. These state what it is for a science to be committed to characters:

1. Character-Species Separation (CSS): Characters and species are metaphysically distinct evolving units in evolution. They have distinct identity and persistence conditions through evolutionary time, and their boundaries do not map onto each other except contingently. Lineages of species and of characters are metaphysically distinct, even if intertwined

<sup>&</sup>lt;sup>4</sup> The issues of character individuation and novelty have garnered increasing attention as major concerns in their own right. See, e.g., Bock and Cardew 1999, Butler and Saidel 2000, Hall 2003, Griffiths 2006, 2007; Brigandt 2003; Novick 2018; Erwin 2021; Muller and Wagner 1991; Peterson and Muller 2016; Shubin et al. 2009; DiFrisco et al. 2020; Love 2008, 2015, 2018; Brigandt and Love 2012.

methodologically and historically – for example, when using homology as evidence for phylogenetic hypotheses, or when the appearance of a novel character generates new taxa in adaptive radiation. From a metaphysical perspective, a tree of life based on characters rather than species would be equally valid (if strange-looking). At the very least, there is no *a priori* reason to think major transitions of characters will coincide with those of species or organisms arranged by mereologically complex integration of replicating individuals (Szathmary and Maynard Smith 1995; Szathmary 2015).

Note that a character that is unique to one species – a species-level autapomorphy – is still a character; cross-species individuation of characters makes it possible for such autapomorphies to be *a posteriori*. Claims of autapomorphy are usually made at taxonomic levels (or within clades) more inclusive than that of species, but in what follows I will use "autapomorphy" as a specieslevel concept due to the prevalence of claims of human cognitive uniqueness in cognitive science. A human uniqueness claim comes for free if an autapomorphy claim is made for hominins, given that all other hominins are extinct.

2. Character-Phenotype Separation (CPS): Characters and phenotypes are metaphysically distinct units in evolution. Evolutionary explanation invokes two distinct basic types of traits to explain, and be explained by, descent with modification: characters and phenotypes. These two types obey distinct individuation principles, require distinct explanations, and serve distinct explanatory purposes. Phenotypes are possessed by individual organisms and ground each organism's fitness for survival in its environment. They integrate features specific to an individual (e.g., a human's chipped canine tooth) and its species (e.g., the human canine-tooth phenotype), and features that are shared across species (e.g., the canine tooth character). Characters are individuated across species and are needed to explain stable patterns of traits across species

(often despite vast adaptive differences) and limits to phenotypic variation within species that arise from their evolutionary heritage.<sup>5</sup> Of course, many comparative explanations will invoke both historical and environmental factors, or "ancestry" and "adaptation" (Currie 2021). But the character-phenotype relation itself may be understood as a special case of the determinabledeterminate relation: a phenotype is a way of being a character (or character state), and phenotypes determine characters (or express them, to follow a common biological usage). What makes this a special case is that it involves a way of being structured by ancestry, whereas the determinabledeterminate relation in general is ahistorical.<sup>6</sup>

A consequence of CPS is that terms such as "the human brain" and "the primate brain" have very different referents. The former term refers to a species-typical phenotype, a statistical norm derived from measures of the individual organs in human organisms. Evolutionary theory does not quantify over species-typical phenotypes. Such terms represent a convenient way for us to talk about a trait as it presents in all normally developed organisms in a species. (I will take advantage of this convenience below.) The latter term refers to a morphological character, of which disproportionately large frontal lobes are characteristic (Dunbar and Schultz 2007). Evolutionary

<sup>&</sup>lt;sup>5</sup>The boundaries of characters at different levels of biological organization also align contingently (Ereshefsky 2012 calls this "hierarchical disconnect"). They evolve at different rates, homology at one level does not entail homology at others, and co-evolution often occurs with temporal lags between appearances of novel characters at distinct levels (Erwin 2021; Corballis 2000; Ginsburg and Jablonka 2010). For example, the Pax-6 gene is homologous in mammals and flies and plays a key role in the development of mammalian camera and fly compound eyes, but the eyes themselves are nonhomologous (Wagner 2001; Shubin, Tabin, and Carroll 2009).

<sup>&</sup>lt;sup>6</sup> The standard example is the relation between being red and being colored (Wilson 2021). As with other determinates, being one determinate (e.g., a human canine tooth, being red) rules out being another (e.g., a narwhal canine tooth, being blue), and the relation is not conjunctive (e.g., a human canine tooth is not a canine tooth plus some independent properties, whereas a human is a mammal plus some independent properties, such as having cognitive states).

theory does quantify over morphological characters. The term "trait" generalizes over this critical distinction.

CSS and CPS jointly spell out an ontological commitment to characters that is as fundamental to evolutionary explanations as more familiar commitments to organisms, species, and phenotypes. They ground cross-species comparisons of biological units at any level of biological organization. As noted, research on characters has tended to emphasize the characters of relatively easily individualized parts and organs of mature organisms. Neglect of behavioral characters has not always been benign, but behavioral characters have been defended in classical ethology (Lorenz 1965; Tinbergen op.cit.) and in biology (De Queiroz and Wimberger 1993; Rendall and Di Fiore 2007; Di Fiore and Rendall 1994; Greene 1999; Masters 2007; Hall 2012). The innovation of Lorenz and Tinbergen was precisely to conceptualize behaviors as expressions of behavioral characters (Burkhardt 2005). This made behavior a target of Tinbergen's four questions for explaining any biological trait: mechanism, function or survival value, ontogeny, and phylogeny.<sup>7</sup> The phylogeny question entailed explaining behavior in terms of characters and homologies. CSS lies behind the realization in behavioral ecology that distinct species are not necessarily independent data points for the purpose of defining behavioral characters, and CPS is implicit in the fact that behavioral homology has been controversial but behavioral phenotypes have never been.

However, cognitive character research remains largely a task for the future – a reflection of the disconnect of psychology from biology with respect to what is entailed by their shared

<sup>&</sup>lt;sup>7</sup>Thus, the question of *why* primates have disproportionately large frontal lobes can be disambiguated into complementary queries using Tinbergen's (op.cit.) framework. The phylogeny question asks about the ancestry of the primate brain, and will have competing explanations in terms of characters and homology. Other queries, such as what function large frontal lobes have, will have competing explanations in terms of adaptive pressures (e.g. Dunbar and Shultz 2017).

allegiance to evolution. Philosophers have explored extensions of morphological ideas to behavioral characters (Ereshefsky 2007; Sober 2005), and have discussed cognitive homology, often with respect to basic emotions and sense perception (Griffiths 1997, 2006, 2007; Matthen 1998, 2000, 2007; Keeley 2002; Ereshefsky op.cit.; Bergeron 2021). Given an explicit and operative commitment to characters, cognitive science would be in a position to extend recent biological and philosophical research on characters to the "high-level" cognitive abilities many consider unique to humans. In the next two sections I show why cognitive scientists should make this commitment.

## 3. Three Implications of CSS and CPS: Uniquely Human in What Sense?

In principle, CSS and CPS readily apply to cognition once we agree cognition evolved. And if cognitive abilities help explain behavior, multi-level explanations of the co-evolution of behavior and morphology will omit an important explanatory factor without the contribution of cognitive characters. However, integrating characters into cognitive science would involve profound changes in how we think about and investigate cognition. For a simple illustration, in comparative evolutionary biology no one thinks the felid skull (let alone the *F. domesticus* skull) is the reference skull for skullhood, in comparison to which other species' skulls are not fullfledged skulls. In contrast, the idea that a human-typical cognitive phenotype defines that cognitive ability is implicit whenever nonhuman species' abilities are described as not full-fledged in comparison. This and similar descriptors may rest implicitly on metaphysically loaded presuppositions in which the human cognitive abilities are the reference abilities.<sup>8</sup>

<sup>&</sup>lt;sup>8</sup> In principle, the same mistake would be made whenever any species-typical phenotype is used as the reference type in relation to which other species' traits are less than full-fledged. But the mistake is rare outside of human cognitive phenotypes. For example, pigeon visual systems do not

In this section and the next I outline four implications of CSS and CPS for cognitive science. In this section, I present three implications and their impact on the "continuity/discontinuity" debate regarding the relation between human and nonhuman cognition (e.g. Penn et al. 2008; Premack 2007). I also illustrate how cognitive characters are being introduced into research frameworks, implicitly or explicitly. In the next section, I present the fourth implication and its impact on the "what is cognition?" debate regarding the extent of cognition in the biological world (e.g., Adams 2017; Lyon et al. 2021). This involves examining the interaction of independent commitments to evolution and functionalism as the dominant metaphysics of mind.

The first implication is that it is unjustified to infer that *any* species, human or otherwise, has a cognitive character uniquely just because it is a unique species. Even if a character is novel, it does not follow that it is an autapomorphy. As a result, claims of human cognitive uniqueness or distinctiveness are critically ambiguous: an ability is necessarily human if the claim is about a species-typical phenotype but contingently human if the claim is about a character. Species-typical phenotypes are trivially unique to a species. It is far from trivial to establish that the phenotypes typical of a species express a unique character. Thus, when talking of cognitive abilities, any use of the qualifier term "unique" automatically entails a need for clarification: unique as a phenotype, or unique as a character?

The second implication is that it is unjustified to infer from intuitively vast behavioral differences to distinct cognitive characters, let alone to non-trivial human cognitive uniqueness.

need a land-based reference point to get distance-data about things in the sky, whereas the human visual system does (Matthen 2007). We do not however claim that the pigeon visual system is full-fledged while the human system is not.

We judge vast differences in behavior between humans and nonhumans, but such judgments do not fix their nature and significance for cognitive character individuation. Some might object that a conceptual framework in which human phenotypes do not suffice to individuate cognitive abilities is a non-starter (e.g. Bennett and Hacker 2003). But using human and only human behavior as criterial of cognitive characters gets things exactly backwards. Only after it has been established that a behavioral character is an autapomorphy can observation of that behavior justify inferring to a cognitive autapomorphy (assuming a 1:1 correspondence for simplicity).

The third implication is that the use of human-typical cognitive phenotypes as standards or reference abilities for cognition across species violates evolutionary explanatory methodology. The metaphysical foundation of the human cognitive standard is the denial of CSS and CPS for cognition. One can reject the Scala Naturae's claim that "high-level" cognition is uniquely human yet leave this foundation untouched if human cognition retains its standard-setting role.<sup>9</sup> Comparative cognition has often involved problematic cross-species comparisons that use this standard, with well-known poor methodological and empirical results (Shettleworth 1993, 2012; Cartmill 1990). CSS and CPS entail complete repudiation of this explanatory methodology. Human cognitive phenotypes can remain important sources of evidence and insight regarding cognitive abilities, but they cannot individuate them.

The hand character furnishes a simple analogy for what abandoning the human cognitive standard involves. This character is a species-neutral standard for determining whether a morphological structure typical of a species is or is not a hand. If two such phenotypes count as hands, adaptive hypotheses can be used to explain the species-typical differences, but their status

<sup>&</sup>lt;sup>9</sup> The Scala Naturae itself contained the idea of inferior grades of "high-level" cognitive capacities in the form of racist distinctions in intelligence that created a linear ranking of humans within our species' rung. Darwin himself was not exempt from this legacy of cognitive racism (Jeynes 2011).

as hands is not affected by the comparison however different the phenotypes might be. Similarly, cognitive phenotypes either are or are not expressions of the same cognitive character or character state (if more than one). If they are, adaptive hypotheses may explain potentially vast differences between the species-typical cognitive phenotypes that express this character, but judgments that some of them are not full-fledged are metaphysically incoherent. In sum, when our goal is to explain human cognition, we first need to conceptualize what we think humans have in terms of what cognitive characters we think human cognitive phenotypes express.

These three implications of CSS and CPS for cognitive science – that distinct species do not thereby express distinct cognitive characters; that vast behavioral differences are compatible with identical cognitive characters; and cognitive characters determine what is, and what is not, the same cognitive ability across species – show the extent to which the character concept is not integrated into cognitive theorizing or empirical research. Human phenotypes may still be treated as reference abilities. For example, Penn et al. 2008 argue for discontinuity between relational abilities of modern humans and all extant nonhuman species starting *ex hypothesi* from Newell and Simon's physical symbol hypothesis as a theory of a human competence. It is *a priori* impossible for nonhuman species to meet this human standard. Similarly, the claim that the latest major transition in evolution is to *human* culture and the development of *human* language, with animal cultures "limited" in comparison, is at best ambiguous (Szathmary 2015).<sup>10</sup> If the transition is framed in terms of characters, animal languages and cultures are not "limited": the characters either are human cognitive autapomorphies, or they are not. If it is a transition to human species-typical phenotypes, it is metaphysically incoherent within the framework of evolutionary theory.

<sup>&</sup>lt;sup>10</sup> McShea and Simpson (2011) note the theoretical inconsistency of the final transition to human society and language, as it involves a change of criteria from an increase in hierarchy to an increase in information transmission.

Recent comparative theorizing provides examples of how ambiguous cognitive hypotheses can be reformulated to explicitly reject the human cognitive standard and fully embrace evolutionary explanatory methodology. A fruitful method (if not the only one) is to analyze human-typical cognitive phenotypes into components and reconceptualize the components in terms of characters, thus embracing CSS and CPS (perhaps implicitly). This adjustment rules out anthropocentric and a prioristic interpretations of hypotheses of human cognitive uniqueness. I will illustrate how this method works using recent research in episodic memory and language, including sociocultural hypotheses of the development of language (among other "high-level" cognitive abilities). The first example is brief, the latter more extended.

In the case of episodic memory, Tulving 2005 hypothesizes that episodic memory is unique to humans on the basis that autonoetic consciousness is unique to humans (see also Suddendorf and Corballis 2015). These cognitive abilities are unique to humans "in the sense that the mental capacities that define them do not exist in quite the same full-fledged form in other species" (op.cit.: 5). Tulving "hastens to clarify" that his uniqueness claim "is not meant as a delayed rearguard action in support of the myth of the *scala naturae*" (op.cit: 4), although it remains unclear what justifies his claim that the human form is full-fledged, thus implying that the others are not.

Clayton and Russell 2009 respond to Tulving by proposing that re-experiencing involves the egocentric or viewer-relative spatial perspective encoded non-conceptually in the original experience. Thus, "just as human episodic memory will inherit the character of human experience, so will avian episodic memory inherit the character of avian experience" (op.cit.: 2331; the term "character" here is the non-technical "quality" sense). An unambiguously empirical debate now emerges. Unlike Allen and Fortin (2013), Clayton and Russell agree with Tulving that autonoetic consciousness is a necessary component of episodic memory, but disagree that autonoetic consciousness is a human cognitive autapomorphy. Tulving's claim about what is full-fledged and what isn't, which in fact presupposes his human uniqueness conclusion, can be quietly forgotten.<sup>11</sup>

While episodic memory may or may not be unique to humans, natural language has long played a central role in establishing human cognitive uniqueness in general and in explaining differences between human and nonhuman minds (Pinker and Bloom 1990; Bolhuis et al 2014; Hauser et al. 2002; Christiansen and Kirby 2003). It is therefore consequential to reconceptualize language in accordance with CSS and CPS. The term "language" itself is often restricted in reference to the human species-typical communication system, such that talk of nonhuman "language" is a misuse of the term. The character concept eliminates this verbal source of potential confusion. "Language" refers to an evolved ability, and the human species-typical communication system phenotype expresses the language character.<sup>12</sup> If nonhuman species-typical communication system phenotypes express this character, they are languages; if not, human language is an autapomorphy. Either way, the human language phenotype can be the starting point for analysis without also fixing what it is to be a language and so what "language" refers to.

We can then turn to the substantive work of defining the language character and explaining how a phenotype that expresses it comes to have the species-typical form or forms it takes. Two aspects of language considered essential to it include reference and syntax. The former involves

<sup>&</sup>lt;sup>11</sup> Such conceptual hiccups are not limited to those on the "discontinuity" side. Consider Savage-Rumbaugh and Lewin's (1994) *Kanzi: The ape at the brink of the human mind*: Kanzi's mind is no more at the brink of the human mind than his hands are at the brink of the human hand.

<sup>&</sup>lt;sup>12</sup> I simplify matters for illustrative purposes, since language interacts with other cognitive abilities, and the voluminous literature on language and its evolution cannot be reviewed here. To give one example, if an ability to learn language requires understanding communicative intentions, then either a species that does not possess this ability cannot learn language, or they have another language acquisition mechanism. So communicative intentions must also be reconceptualized so that nonhuman species are not ruled out *a priori* from having them (Moore 2017, Townsend et al. 2017). Whether a communication system must be learned to count as a language is a further issue.

using specific linguistic units to pick out or represent items or states of affairs in the world, the latter recombining linguistic units to express distinct complex meanings. That some nonhuman communication systems have reference is now widely accepted, and uniqueness claims have shifted to emphasizing syntax. But to be consistent with evolutionary explanatory methodology, syntax must be defined without using human syntax as the reference ability. Balari and Lorenzo propose exactly this (2015; see also Margoliash and Nusbaum 2009).

Syntax has been theorized in terms of a Merge operation that combines linguistic units, in particular into recursive or hierarchical linguistic structures (Chomsky 2013, Hauser et al 2002). Balari and Lorenzo reconceptualize the Merge operation as a character. In humans, the Merge operation interacts with an enhanced working memory ability and perhaps with certain features of the linguistic objects that are combined. This enables human Merge to form the hierarchical structures with intersymbol dependencies characteristic of the human syntax phenotype and thus the human language phenotype. The same Merge operation in a bird species or genus (e.g., Suzuki et al. 2016, Laine et al. 2016) might operate with fewer memory resources, or its objects may differ relevantly from the human objects. These differences can yield the observable differences in combinatorial complexity in birdsong phenotypes and the human language phenotype even though they both express the Merge character characteristic of language.

As a result, as Balari and Lorenzo (2015: 9) put it, the relative complexity of human syntactic structure is no longer the "Rubicon of sorts" between humans and other species. They agree with Bolhuis et al. (2014) that Merge is characteristic of syntax and that syntax is characteristic of language, but disagree that hierarchical syntax is characteristic of language. Instead, hierarchical syntax is characteristic of the human-typical phenotypic expression of the Merge character and the language character, which may or may not be human cognitive

autapomorphies.<sup>13</sup> We can now distinguish unambiguously empirical hypotheses about syntax and language as human cognitive autapomorphies from ambiguous hypotheses that only humans have syntax or that language is unique to humans. This clarification promotes integration of cognitive science with biological research into possible homologies in brains and vocalization structures underlying language processing and production (e.g., Corballis 2017; Jarvis 2019).

The question "How did language evolve?" now raises two distinct groups of substantive questions (which may overlap methodologically). One centers on the language character. For example, is it a human autapomorphy? If not, what innovations might nonhuman languages express? From what character did it evolve, and when? The other group centers on language phenotypes. For example, which aspects of the human form of life contribute to the normal development of the human language phenotype? How are these aspects related to the development of the communication phenotypes of other species, whether or not they are languages? The status of language as a human autapomorphy is irrelevant to this second group of questions.

Sociocultural theories of human cognition add further complexity to these questions. This broad family of theories holds that human cognitive abilities, including language, are a result of uniquely human cultural features.<sup>14</sup> The uniquely human cultural features explain the uniquely

<sup>&</sup>lt;sup>13</sup> Balari and Lorenzo argue that human language may be a novel character state, if not a novel character; they follow Wagner 2014 in linking distinct types of evolutionary novelty to characters and character states. Others reserve the concept of novelty for characters and character states (usually structural), using the concept of innovation for phenotypes (usually functional or adaptive) (Erwin 2021; Love 2008). In any case, I am not arguing that human language is not novel as a character or as a character state – that is a matter of individuating the relevant characters, and is certain to be a contentious issue going forward. I *am* arguing that its status as a novelty (or not) *becomes* an *a posteriori* issue by virtue of adopting a character-based concept of syntax.

<sup>&</sup>lt;sup>14</sup> For some sociocultural theories of cognition, see Boyd and Richerson 1985; Deacon 1997; Tomasello 1999; Sterelny 2003, 2007; Whiten and Erdal 2012; Heyes 2018, 2019; Kempe et al. 2014; Beller et al. 2020; Kirby et al. 2007; Avital and Jablonka 2000. Like that of language evolution, this literature is also voluminous and cannot be reviewed here.

human cognitive abilities. For these theories, integrating characters requires conceptualizing culture, along with language, mind-reading, and so on, in terms of CSS and CPS.

This difference can be illustrated with Heyes' (2018) defense of "distinctively human cognitive mechanisms", or "cognitive gadgets", on the grounds that they are shaped by human culture. Language is among these cognitive gadgets. Given CSS and CPS, Heyes' proposal is compatible with other species having the same cognitive gadget-characters expressed in their own distinctively species-typical gadget-phenotypes, although the explanation of their gadgetphenotypes need not also involve culture (Whiten 2019). Alternatively, it may be understood as the complex empirical hypothesis that the cognitive gadget-characters are human cognitive autapomorphies, and that the reason they are is because the relevant features of human culture are human cultural autapomorphies. CSS and CPS counsel caution regarding these hypotheses. The features of human cultural phenotypes that are highly adaptively significant to the human form of life do not make these features cultural autapomorphies. Significance to us is not significance from an evolutionary (phylogenetic) perspective. Other animals have cultures and forms of social learning and their cognitive abilities may be explained by gene-culture co-evolution (Whitehead et al. 2019). In addition, human cultural autapomorphies do not entail human cognitive autapomorphies. The relevant features of human culture may expose to selection latent possibilities in cognitive characters that existed prior to the origin of the hominin line. Lloyd (2004) points to Kanzi's spontaneous learning and use of lexigrams as an example of a latent language ability released in the novel social context in which his mother was being taught to use lexigrams. On this view, human cultural autapomorphies explain human cognitive phenotypes, but the latter are not cognitive autapomorphies.

The key point is that these hypotheses must be framed within an evolutionary conceptual framework that explicitly rules out using human phenotypes as standards for individuating cognition and culture. Characters enable us to distinguish hypotheses of human cultural and cognitive autapomorphy from hypotheses that seek to explain unique features of human cognitive phenotypes in terms of unique features of human cultural phenotypes. The former hypotheses are intrinsically comparative, the latter are not. Given CSS and CPS, non-trivial evolutionary discontinuity does not come along for free with a species boundary, and continuity is compatible with phenotypes that are vastly different for reasons of vital adaptive significance. It remains true that species with shared ancestry in other respects need not have the same cognitive abilities (Bolhuis and Wynne 2009). But if humans do possess a "quality of mind" (Corballis and Lea 2000) unique to the human species *as a character*, that would be a lagniappe.

#### 4. A Fourth Implication: How Can Evolution and Functionalism Play Well Together?

The fourth implication of CSS and CPS I will emphasize is that only a substrate-dependent special case of functionalism is biologically legitimate in cognitive science in the light of evolution. The relevant contrast here is with the way functionalism – the dominant metaphysics of mind – appears to be taken for granted in hypothesized extensions of cognitive abilities to many biological entities whose behavioral phenotypes are not at all similar to human phenotypes (e.g. Adams 2017; Lyon et al. 2021; Calvo and Keijzer 2009; De Waal and Ferrari 2010; Baluska and Levin 2015). Such extensions by way of functional definitions – e.g. to plants, slime moulds, bacteria, and so on – are a significant motivation for the "What is cognition?" debate.<sup>15</sup> In what

<sup>&</sup>lt;sup>15</sup>Another motivation is the question of whether some realizers extend beyond an entity's boundary. While the issue of the range of cognitive ascriptions across species and this boundary

follows I will show how CSS and CPS make this freewheeling use of functional ascriptions untenable. Abandoning human-based chauvinism in our ascriptions to biological entities need not lead to an unconstrained liberalism (to borrow Block's 1978 terms). Instead, when distinguishing species that have a given cognitive ability from those that don't, we can rely on the same theoretical framework that grounds the drawing of similar distinctions and distributions of non-cognitive traits.

Functionalism holds that mental states (or cognitive abilities) are functional roles comprised of behavioral inputs and outputs and interactions between mental states (or internal processing states). In principle, these roles can be filled or realized by (e.g.) human, reptilian, and mollusc brains, Swiss cheese, Martian stuff, silicon-based computers, and ghostly nonmaterial substances (e.g. Putnam 1967, 1975). Even presupposing a commitment to materialism, building any particular material realization into a functional role places restrictions on multiple realizability, a core tenet of functionalism. Actual functional ascriptions are certainly *limited*, but not systematically constrained, by implicit interpretations of the behaviors cited in the role. For example, one interpretation of "wincing" in a functional definition of pain may hold that specific behaviors of molluscs, computers, and xenobiological entities count as "wincing", while another may rule them out. Disageement over cases often turns on such clashing interpretations of behavior, including, in the case of plants, whether they behave at all.

In contrast, even when restricting our attention to evolved biological realizers, CSS and CPS entail that the behaviors and internal processes that comprise the functional roles must be interpreted as phenotypes that express behavioral and internal-processing characters. And due to

issue are frequently discussed together, my concern is solely with respect to the range question, which is prior to the boundary issue.

the co-evolution of behavior and morphology (among other interlevel interdependencies), this means that the phenotypes and characters will be substrate-dependent. The link between structural and behavioral phenotypes and characters need not be close, but denying any such link is tantamount to saying behavior does not evolve (as Rendall and DiFiore op.cit.: 505 point out in their defense of behavioral homology).<sup>16</sup> In other words, the only form of functionalism consistent with evolution is one that denies medium-independence, and in which the functional roles evolve along with their realizers. Assimilating functionalism into an evolutionary explanatory framework requires adopting and making explicit these constraints on the biological plausibility of functional ascriptions.

This is a major and pressing task for all sides in the "What is cognition?" debate, but is best illustrated by considering what it entails for the basal cognition approach (Lyon et al. op.cit.; Lyon 2006). This is because basal cognition, in a plausible interpretation of its positive proposal, is the empirical polar opposite of and genuine competitor to *a posteriori* hypotheses of human cognitive uniqueness discussed in Section 3.

Basal cognition holds that all biological entities have cognitive abilities. It is motivated by the rejection of the "human standard" in cross-species cognitive comparisons (Lyon and Keijzer 2007), exactly as CSS and CPS require.<sup>17</sup> Advocates employ functional definitions to ascribe

<sup>&</sup>lt;sup>16</sup> In specific cases, a structural character may be necessary for individuating a behavioral or cognitive character, for example in relation to the senses (e.g. Keeley 2002). However, co-evolution and substrate-dependence motivate blurring the structure-function divide in at least epistemological ways, such as when researchers use genetic, developmental, and morphological homologies to support inferences to homologous behavioral and cognitive characters (e.g. Jarvis 2019; De Waal and Ferrari 2010) or to counter claims of uniquely human cognitive abilities based on allegedly unique human brain structures (Herculano-Heuzel 2012; Barton and Venditti 2013; Olkowicz et al. 2016; Logan et al. 2018).

<sup>&</sup>lt;sup>17</sup> What basal cognition is offering in place of the human standard is not clear, as advocates appear conceptually divided in fundamental ways. This includes the issue of whether cognitive terms are used "non-metaphorically" for many simple entities (e.g. Lyon et al. op.cit.: 2) or whether such

cognitive abilities across all these life forms – for example, decision making is "the ability to combine information from multiple sources and act, typically in furtherance of an implicit or explicit goal", anticipation is "the capacity to predict what is likely to happen next based on an early stimulus", and so on (Lyon et al. op.cit.: Table 1). Combined with CSS and CPS, this is to assert that all an organism must do to have basal cognitive abilities is to express the relevant behavioral characters in its behavioral phenotypes.

However, this degree of freedom of behavior from structural constraints is highly implausible from an evolutionary perspective. By this hypothesis, major structural transitions – e.g., from prokaryote to eukaryote and from unicellularity to multicellularity – may make no difference to basal cognitive abilities despite the difference they make to behavior. This does not make basal cognition false, but what traditional functionalism blithely condones evolution does not. So as an empirical position, basal cognition's explicit core claim of cognition in all biological entities appears to be that we have good reason to posit behavioral characters that transcend all structural transitions in phylogeny, and that these behavioral characters, and the cognitive abilities (functional roles) they define, are identical in plants, protazoa, and people, *inter* all other biological

uses are merely "as if" and a matter of personal choice (e.g. Lyon et al. op.cit.: 4). I discern at least two basic forms, which agree on rejecting the human standard and including all evolved biological entities within the scope of cognitive ascriptions. Some advocates are biocyberneticists, who apply the cybernetic framework to all evolved biological entities (e.g. Manicka and Levin 2019; Levin et al. 2021). In this case, basal cognition's scope is a restriction from (or subset of) the domain of all entities subject to cybernetic explanations. At least some in this camp appear to embrace Dennett's intentional stance in that it is fruitful to treat these entities as agents (e.g. Levin and Dennett 2020). Other advocates take basal cognition's starting point as evolutionary biology; in this case, its scope is an expansion from a few biological entities to all those subject to evolutionary explanations. At least some in this camp hold that the ascriptions of cognitive abilities in the "basic toolkit" are the same across unicellular and multicellular organisms (e.g. Lyon 2015). In the text, I have taken on board the latter interpretation, because it is consistent with basal cognition's role in the ongoing debate about the extent of cognition (as Adams 2017 makes clear), and it links basal cognition essentially to biology and evolutionary explanation.

*alia*. In sum, what is "basal" in basal cognition are these alleged behavioral characters, not any apparent connection to mereologically simple organisms. Mereological simplicity – or complexity, for that matter – may be irrelevant.<sup>18</sup>

Do we have good empirical (and theoretical) reasons to posit such maximally general behavioral characters, and are we able methodologically to establish their presence across all phyla? There can be such characters of complete generality, true of all life (Platnick 1979: 543). But while traditional functionalism licenses ascribing behavioral and cognitive characters anywhere, evolution requires grounds for claims of behavioral character identity that go beyond this fact. For basal cognitivists, this means drawing a principled, if fuzzy, line between biologically and artificially realized functional roles, since artificial realizers need not evolve. It would also mean indicating how basal cognitive characters constrain the derived cognitive characters that appear later in phylogeny. And the main empirical alternative would not be a return to the human cognitive standard and human cognitive uniqueness, but an approach that works backwards from

<sup>&</sup>lt;sup>18</sup> I say "may be" because basal cognition (in its biology-based form: see fn. 17) can be elaborated in a way grounded in CSS and CPS that takes at least some structure into account. A straightforward interpretation of the claim of a "basic toolkit" of cognitive characters true of all of life is that this toolkit existed in the Last Universal Common Ancestor and is homologous in all descendant clades that possess it (or at least one component of it). An alternative interpretation that takes structure into account might hold that prokaryotes have a derived, novel cognitive "toolkit" and eukaryotes have another, and these are homologous within these broad clades but only analogous to each other. In this case, the LUCA must be ascribed an ancestral "cognitive" toolkit as well, for few would disagree with the idea that cognitive abilities are derived, novel characters: the central question of the "What is Cognition?" debate (in my terms) is precisely whether cognitive characters are found only in a few higher clades (if not just hominins) or much more widely, as basal cognition asserts. In the text, I articulate what this assertion amounts to in terms of the straightforward interpretation; the alternative is possible, but creates new problems for the view. For example, a eukaryote-cognition-toolkit would take structure into account and would not be maximally general. But why stop at multicellularity? The problem is that the more structure matters, the less "basal" basal cognition becomes.

the more empirically accessible derived cognitive and behavioral characters to posit the basal ones, which plausibly may have appeared only during or after the Cambrian explosion.<sup>19</sup>

However, my aim here is not to settle the "What is cognition?" debate or argue against basal cognition. It is to illustrate how CSS and CPS impose significant constraints on our use of functional ascriptions of cognitive abilities than is permitted (even encouraged) by traditional functionalism. In particular, our ability and willingness to employ functional ascriptions far outstrips our ability to identify behavioral characters, especially characters that transcend all major structural transitions in phylogeny. Such ascriptions may pick out superficial similarities, and may prompt drawing analogies between structures to support the functional ascriptions (e.g. Calvo and Keijzer op.cit.). But structural analogies are as unconstrained as traditional functional roles (e.g. Boyden 1947). CSS and CPS prompt research into the evolving functional roles themselves.

#### **Conclusion: From Scala Naturae to Selva Cognitiva**

Two fundamental principles built into the ontology of evolution articulate what it means to commit to the character concept. This concept represents evolutionary continuity of traits across species, despite possibly vast phenotypic differences but without ruling out discontinuity. Our tradition of a necessary connection of cognitive traits with the human species has made it difficult to adopt this ontology even while accepting that cognition evolved. Cognitive researchers would do well to replace their uses of "trait" (or "feature") with either "character" or "phenotype", as

<sup>&</sup>lt;sup>19</sup> When weighing evidence as to whether cognitive abilities are homologous or analogous, De Waal and Ferrari (op.cit.: 202) suggest as a "most parsimonious Darwinian assumption" that if closely related species (octopus and squid, human and ape) "show similar solutions to similar problems, they probably involve similar cognitive mechanisms" – that is, cognitive homologies within higher (relatively more terminal) clades. This view is consistent with the ontologically conservative approach mooted in the text, although in no way is basal cognition ruled out.

they intend, to encourage awareness of characters and ensure their positions mesh conceptually with the rest of biology.

I have also pointed out some implications for cognitive science of adopting the character concept. Claims of human cognitive uniqueness must depend on these principles to be unambiguously empirical. Uniqueness and novelty are not ruled out, but non-trivial human cognitive uniqueness should not be a foregone conclusion. Cognitive science should also be chary of reifying phenotypic variation in its characters. At the same time, in the light of the widening scope of behavioral and cognitive research across biological species, phenotypes may be grouped as common solutions to ecological problems as more knowledge is gained that might justify positing behavioral and cognitive characters and homologies across more and perhaps all species.

Finally, characters enable us to disambiguate the question "What makes human cognition special?" into two research questions: "What is human cognition?" and "In what ways is human cognition distinct from bonobo cognition, honeybee cognition, scrub jay cognition, etc.?" These questions involve distinct explananda: the human cognitive phenotype (or phenotypes: Boesch 2007) versus cross-species comparisons dependent on cognitive characters. One can agree with current leading hypotheses that what makes human cognition special is the accumulation and transmission of acquired knowledge via cultural mechanisms over generations, *and* hold that it is an open question if and how this fact matters to the individuation of the cognitive characters underlying our minds and behavior, let alone their status as human autapomorphies.

To paraphrase Wagner (2014: Ch. 1, 33): Only when we can understand the conservation and development of cognitive characters do we have a chance of successfully integrating cognitive science with other sciences conducted in the light of evolution. We are not quite there.

# **References (2,200 words)**

Adams, F. (2017). Cognition wars. Studies in History and Philosophy of Science 68: 20-30.

Allen, T. and N. Fortin (2013). The evolution of episodic memory. *PNAS* 110 (suppl.2): 10379-10386.

Avital, E. and E. Jablonka (2000). *Animal traditions: Behavioural evidence in evolution*. Cambridge: Cambridge University Press.

Balari, S. and G. Lorenzo (2015). It is an organ, it is new, but it is not a new organ: conceptualizing language from a homological perspective. *Frontiers in Ecology and Evolution* 3 (Article 58) 3-18.

Barkow, J., L. Cosmides, and J. Tooby (1992). *The Adapted Mind: Evolutionary psychology and the generation of culture*. Oxford University Press.

Barton, R. and C. Venditti (2013). Human frontal lobes are not relatively large. *PNAS* 110 (22): 9001-9006.

Bennett, M. and P.M.S. Hacker 2003. *Philosophical Foundations of Neuroscience*. London: Blackwell.

Beller, S., A. Bender and F. Jordan (2020). Editors Review and Introduction: The cultural evolution of cognition. *Topics in Cognitive Science* 12 (2): 644-653.

Bergeron, V. (2021). Carving the Mind at its Homologous Joints. *Biology and Philosophy* 36 (4): 1-16.

Baluska, F. and M. Levin (2016). On having no head: cognition throughout biological systems. *Frontiers in Psychology* 7: 902.

Block, N. (1978). Troubles With Functionalism. In C. Savage, ed., Perception and Cognition: Issues in the Foundations of Psychology (Minneapolis: University of Minnesota Press): 261-325.

Bock, G. and G. Cardew, eds. (1999). *Homology. Novartis Foundation Symposium 22*. Chicester: John Wiley and Sons Ltd.

Boesch, C. (2007). What makes us human (H. sapiens)? The challenge of cognitive cross-species comparisons. *Journal of Comparative Psychology* 121 (3): 227-240.

Bolhuis, J. and C. Wynne (2009). Can evolution explain how minds work? Nature 486

Bolhuis, J., I. Tattersall, N. Chomsky, and R. Berwick (2014). How could language have evolved? *PLoS Biology* 12 (8): e1001934.

Boyd, R. and P. Richerson (1985). *Culture and the Evolutionary Process*. Chicago: Chicago University Press.

Boyden, A. (1947). Homology and Analogy: A critical review of the meanings and implications of these concepts in biology. *The American Midland Naturalist* 37 (3): 648-669.

Brauer, J., D. Hanus, S. Pika, R. Gray, and N. Uomini (2020). Old and new approaches to animal cognition: there is not "one cognition". *Journal of Intelligence* 8 (28): 1-25.

Brigandt, I. (2003). Homology in Comparative, Molecular, and Evolutionary Developmental Biology: The radiation of a concept. *Journal of Experimental Zoology* (Mol Dev Evol) 299B: 9-17.

Brigandt, I. and A. Love (2012). Conceptualizing evolutionary novelty: Moving beyond definitional debates. *Journal of Experimental Zoology* 318B: 417-427.

Bueno, O., R.-L. Chen, and M. Fagan, eds. (2018). *Individuation, Process, and Scientific Practices*. Oxford: Oxford University Press.

Burkhardt, Jr., R. (2005). *Patterns of Behavior: Konrad Lorenz, Niko Tinbergen, and the Founding of Ethology*. University of Chicago Press.

Butler, A. and W. Saidel (2000). Defining sameness: historical, biological, and generative homology. BioEssays 22: 846-853.

Calvo, P. and F. Keijzer (2009). Cognition in Plants. In F. Baluska, ed., Plant-Environment Interactions, Signaling and Communication in Plants. Berlin: Springer-Verlag.

Cartmill, M. (1990). Human uniqueness and theoretical content in paleoanthropology. *International Journal of Primatology* 11 (3): 173-192.

Christiansen, M. and S. Kirby (2003). Language Evolution: consensus and controversies. *Trends in Cognitive Sciences* 7 (7): 300-307.

Clayton, N., and J. Russell (2009). Looking for episodic memory in animals and young children: Prospects for a new minimalism. *Neuropsychologia* 47: 2330-2340.

Colless, D. (1985). On "Character" and Related Terms. Systematic Zoology 34 (2): 229-233.

Corballis, M. (2017). Language evolution: a changing perspective. *Trends in Cognitive Sciences* 21 (4): 229-236.

Corballis, M. and S. Lea (2000). Are humans special? A history of psychological perspectives. In M. Corballis and S. Lea, eds., *The Descent of Mind: Psychological Perspectives on Hominid Evolution*. (Oxford: Oxford University Press): 1-20.

Deacon, T. (1997). *The Symbolic Species: The co-evolution of language and the human brain.* New York: W.W. Norton and Co.

De Queiroz, A. and P. Wimberger (1993). The usefulness of behavior for phylogeny estimation: Levels of homoplasy in behavioral and morphological characters. *Evolution* 47 (1): 46-60.

De Waal, F. and P. Ferrari (2010). Towards a Bottom-Up Perspective on Animal and Human cognition. *Trends in Cognitive Sciences* 14 (5): 201-207.

Di Fiore, A. and D. Rendall (1994). Evolution of social organization: A reappraisal for primates using phylogenetic methods. *Proceedings of the National Academy of the Sciences USA* 91: 9941-9945.

DiFrisco, J., A. Love, and G. Wagner (2020). Character identity mechanisms: a conceptual model for comparative-mechanistic biology. *Biology and Philosophy* 35:44: 1-32.

Dobzhansky, T. (1973). Nothing in biology makes sense except in the light of evolution. *The American Biology Teacher* 35 (3): 125-129.

Duda, P. and J. Zrzavy (2013). Evolution of life history and behavior in Hominidae: Towards a phylogenetic reconstruction of the chimpanzee-human last common ancestor. Journal of Human Evolution 65: 424-446.

Dunbar, R. and S. Shultz (2007). Understanding primate brain evolution. Philosophical Transactions of the Royal Society B 362: 649-658.

Dunbar, R. and S. Shultz (2017). Why are there so many explanations for primate brain evolution? Philosophical Transactions of the Royal Society B 372: 20160244.

Dupre, J. (2021). The Metaphysics of Biology. Cambridge: Cambridge University Press.

Ereshefsky, M. (2007). Psychological categories as homologies: lessons from ethology. Biology and Philosophy

Ereshefsky, M. (2012). Homology Thinking. Biology and Philosophy 27: 381-400.

Figdor, C. (2018). *Pieces of Mind: the proper domain of psychological predicates*. London and New York: Oxford University Press.

Freudenstein, J. (2005). Characters, states, and homology. Systematic Biology 54 (6): 965-973.

Ghiselin, M. (1976). The Nomenclature of Correspondence: A new look at "homology" and "analogy". In Masterton, B., M. Bitterman, C. Campbell and N. Hotton, eds., Evolution of Brain and Behavior in Vertebrates (Lawrence Erlbaum Associates): 129-142.

Ginsburg, S. and E. Jablonka (2010). The evolution of associative learning: A factor in the Cambrian explosion. *Journal of Theoretical Biology* 266: 11-20.

Grant, T. and A. Kluge (2004). Transformation series as an ideographic character concept. *Cladistics* 20: 23-31.

Griffiths, P. (1997). What Emotions Really Are: The problem of psychological categories. Chicago: University of Chicago Press.

Griffiths, P. (2006). Function, homology, and character individuation. *Philosophy of Science* 73: 1-25.

Griffiths, P. (2007). Evo-Devo Meets the Mind: Toward a developmental evolutionary psychology. In R. Sansom and R. Brandon, eds., *Integrating evolution and development: From theory to practice* (MIT Press): 195-225.

Griffiths, P. (2009). In what sense does 'nothing make sense in the light of evolution'? *Acta Biologica* 57: 11-32.

Greene, H. (1999). Natural history and behavioural homology. In Bock and Cardew, eds. *Homology*. 173-182.

Hall, B., ed. (1994). Homology: The hierarchical basis of comparative biology. Academic Press.

Hall, B. (2003). Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. *Biological Reviews* 78: 409-433.

Hall, B. (2007). Homoplasy and Homology: Dichotomy or continuum? *Journal of Human Evolution* 52: 473-479.

Hall, B. (2012). Homology, Homoplasy, Novelty and Behavior. Developmental Psychobiology.

Hauser, M., N. Chomsky, and W.T. Fitch (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science* 298: 1569-1579

Herculano-Houzel, S. (2012). The remarkable, yet not extraordinary, human brain as a scaled-up primate brain and its associated cost. *PNAS* 109 (suppl.1): 10661-10668.

Heyes, C. (2013). Q&A. Current Biology 23 (3): R98-R100.

Heyes, C. (2018). Cognitive Gadgets. Oxford: Oxford University Press.

Heyes, C. (2019). Precis of Cognitive Gadgets. Behavioral and Brain Sciences *Behavioral and Brain Sciences* 42, e169: 40-42.

Jarvis, E. (2019). Evolution of vocal learning and spoken language. Science 366 (6461): 50-54.

Jeynes, W. (2011). Race, racism, and Darwin. Education and Urban Society 43 (5): 535-559.

Keeley, B. (2002). Making sense of the senses: Individuating modalities in humans and other animals. *Journal of Philosophy* 99 (1): 5-28.

Kempe, M., S. Lycett, and A. Mesoudi (2014). From cultural traditions to cumulative culture: parameterizing the differences between human and nonhuman culture. *Journal of Theoretical Biology* 359: 29-36.

Kirby, S., M. Dowman, and T. Griffiths (2007). Innateness and culture in the evolution of language. *Proceedings of the National Academy of Sciences of the USA* 104 (12): 5241-5245.

Laine, V., T. Gossmann, K. Schachtschneider, C. Garroway, O. Madsen, K. Verhoeven, V. de Jager, H.-J. Megens, W. Warren, P. Minx, R. Crooijmans, P. Corcoran, The Great Tit HapMap Consortium, B. Sheldon, J. Slate, K. Zeng, K. van Oers, M. Visser, and M. Groenen (2016). Evolutionary signals of selection on cognition from the great tit genome and methylome. *Nature Communications* 7: 10474.

Levin, M. and D. Dennett (2020). Cognition All the Way Down. *Aeon.co.* 13 October 2020. https://aeon.co/essays/how-to-understand-cells-tissues-and-organisms-as-agents-with-agendas.

Levin, M., F. Keijzer, F., P. Lyon, and D. Arendt (2021). Uncovering cognitive similarities and differences, conservation and innovation. *Philosophical Transactions of the Royal Society B*: 376: 20200458.

Lloyd, E. (2004). Kanzi, Evolution, and Language. Biology and Philosophy 19: 577-588.

Logan, C., S. Avin, N. Boogert, A. Buskell, F. Cross, A. Currie, S. Jelbert, D. Lukas, R. Mares, A. Navarrete, S. Shigeno, and S. Montgomery (2018). Beyond Brain Size: uncovering the neural correlates of behavioral and cognitive specialization. *Comparative Cognition and Behavior Reviews* 13: 55-89.

Lorenz, K. (1965). Evolution and Modification of Behavior. Chicago: University of Chicago Press.

Love, A. (2007). Functional homology and homology of function: biological concepts and philosophical consequences. *Biology and Philosophy* 22: 691-708.

Love, A. (2008). Explaining Evolutionary Innovations and Novelties: Criteria of explanatory adequacy and epistemological prerequisites. *Philosophy of Science* 75: 874-886.

Love, A. (2015). ChINs, swarms, and variational modalities: concepts in service of an evolutionary research program. *Biology and Philosophy* 30: 873-888.

Lovejoy, A.O. (1936). *The Great Chain of Being: The history of an idea*. Cambridge, MA: Harvard University Press.

Lyon, P. (2006). The biogenic approach to cognition. Cognitive Processing 7: 11-29.

Lyon, P. and F. Keijzer (2007). The Human Stain: Why cognitivism can't tell us what cognition is and what it does. In B. Wallace, A. Ross, J. Davies, and T. Anderson, eds., *The Mind, the Body and the World: Psychology after cognitivism* (Imprint Academic): 132-165.

Lyon, P. (2015). The cognitive cell: bacterial behavior reconsidered. *Frontiers in Microbiology* 6: 264.

Lyon, P., F. Keijzer, D. Arendt, and M. Levin (2021). Reframing cognition: getting down to biological basics. *Philosophical Transactions of the Royal Society B* 376: 20190750, 1-11.

Manicka, S. and M. Levin (2019). The Cognitive Lens: a primer on conceptual tools for analysing information processing in developmental and regenerative morphogenesis. *Philosophical Transactions of the Royal Society B* 374: 20180369.

Margoliash, D. and H. Nusbaum (2009). Language: The perspective from organismal biology. *Trends in Cognitive Sciences* 13 (12): 505-509.

Masters, J. (2007). Taking phylogenetic systematics beyond pattern analysis: Can models of genome dynamics guide predictions about homoplasy in morphological and behavioral data sets? *Journal of Human Evolution* 52: 522-535.

Matthen, M. (1998). Biological universals and the nature of fear. *Journal of Philosophy* 95 (3): 105-132.

Matthen, M. (2000). What is a hand? What is a mind? *Revue Internationale de Philosophie* 54 (214: 4): 653-672.

Matthen, M. (2007). Defining vision: What homology thinking contributes. *Biology and Philosophy* 22: 675-689.

McShea, D. and C. Simpson (2011). The Miscellaneous Transitions in Evolution. In B. Calcott and K. Sterelny, eds., *The Major Transitions in Evolution Revisited*. Cambridge: MIT Press.

Miguel-Tome, S. and R. Llinas (2021). Broadening the Definition of a Nervous System to Better Understand the Evolution of Plants and Animals. Plant Signaling and Behavior 16 (10): e1927562.

Millikan, R. (1964). Language, Thought, and Other Biological Categories. Cambridge: MIT Press.

Moczek, A. (2008). On the origins of novelty in development and evolution. *BioEssays* 30.5: 432-447.

Muller, G. and G. Wagner (1991). Novelty in evolution: Restructuring the concept. *Annual Review* of Ecology and Systematics 22: 229-256.

Neander, K. (2014). *A Mark of the Mental: In defense of teleoinformational semantics*. Cambridge: MIT Press.

Olkowicz, S., M. Kocourek, R. Lucan, M. Portes, W. T. Fitch, S. Herculano-Houzel, and P. Nemic (2016). Birds have primate-like numbers of neurons in the forebrain. *PNAS* 113 (26): 7255-7260.

Owen, R. (1849). *On the archetype and homologies of the vertebrate skeleton*. London: John van Voorst.

Penn, D., K. Holyoak, and D. Povinelli 2008. Darwin's mistake: Explaining the continuity and discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences* 31: 109-178.

Peterson, T. and G. Muller (2013). What is evolutionary novelty? Process vs. character based definitions. *Journal of Experimental Zoology* (Mol. Dev. Evol.) 320B: 345-350.

Piccinini, G. (2020). *Neurocognitive Mechanisms: Explaining biological cognition*. Oxford: Oxford University Press.

Pinker, S. and P. Bloom (1990). Natural language and natural selection. *Behavioral and Brain Sciences* 13: 707-784.

Platnick, N. (1979). Philosophy and the Transformation of Cladistics. *Systematic Zoology* 28 (4): 537-546,

Premack, D. 2007. Human and animal cognition: Continuity and discontinuity. *PNAS* 104 (35): 13861-867.

Putnam, H. (1967). Psychological Predicates. In Capitan and Merrill, eds. *Art, Mind and Religion*. Pittsburgh: University of Pittsburgh Press.

Putnam, H. (1975). Philosophy and our Mental Life. In H. Putnam, Mind, Language, and Reality, Philosophical Papers vol. 2 (London: Cambridge University Press): 291-303.

Rendall, D. and A. Di Fiore (2007). Homoplasy, homology, and the perceived special status of behavior in evolution. *Journal of Human Evolution* 52: 504-521.

Shettleworth, S. 2009. The evolution of comparative cognition: Is the snark still a boojum? *Behavioural Processes* 80: 210-17.

Shettleworth, S. 2012. Modularity, Comparative Cognition, and Human Uniqueness. *Philosophical Transactions of the Royal Society B* 367: 2794-2802.

Sober, E. (2005). Comparative Psychology Meets Evolutionary Biology: Morgan's canon and cladistic parsimony. In *Thinking With Animals: New perspectives on anthropomorphism* (New York: Columbia University Press), 97-99.

Sterelny, K. (2003). Thought in a Hostile World: The evolution of human cognition. Oxford.

Sterelny, K. (2007). Social intelligence, human intelligence, and niche construction. *Philosophical Transactions of the Royal Society B* 362: 719-730.

Suddendorf, T. and M. Corballis (2015). Behavioural evidence for mental time travel in nonhuman animals. *Behavioural Brain Research* 215: 292-298.

Suzuki, T., D. Wheatcroft, and M. Griesser (2015). Experimental evidence for compositional syntax in bird calls. *Nature Communications* 7: 10986.

Tinbergen, N. (1963). On aims and methods of ethology. Zeit. Tierpychol. 20, 410-433. Reprinted in Bolhuis and Verhulst, eds., *Tinbergen's Legacy: Function and Mechanism in Behavioral Biology* (Cambridge: Cambridge University Press), 1-24.

Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.

Townsend, S., S. Koski, R. Byrne, K. Slocombe, B. Bickel, M. Boekle, I. Goncalves, J. Burkart, T. Flower, F. Gaunet, H.-J. Glock, T. Gruber, D. Jansen, K. Liebal, A. Linke, A. Miklosi, R. Moore, C. van Schaik, S. Stoll, A. Vail, B. Waller, M. Wild, K. Zuberbuhler, M. Manser (2017). Exorcising Grice's Ghost: an empirical approach to studying intentional communication in animals. *Biological Reviews* 92: 1427-1433.

Tulving, E. 1972. Episodic and semantic memory. In E. Tulving and W. Donaldson, *Organization of Memory* (Academic): 381-403.

Tulving, E. 2005. Episodic memory and autonoesis: uniquely human? In H. Terrace and J. Metcalfe, eds. *The Missing Link in Cognition: Origins of self-reflective consciousness* (Oxford), 3-56.

Vonk, J. and T. Shackelford (2012). Comparative Evolutionary Psychology: A united discipline for the study of evolved traits. In T. Shackelford and J. Vonk, eds., *The Oxford Handbook of Comparative Evolutionary Psychology* (Oxford): 547-560.

Wagner, G. (2001). Characters, Units, and Natural Kinds: An Introduction. In Wagner, G., ed. *The Character Concept in Evolutionary Biology*. San Diego: Academic Press.

Wagner, G. (2007). The developmental genetics of homology. *Nature Reviews Genetics* 8: 473-479.

Wagner, G. (2014). *Homology, Genes, and Evolutionary Innovation*. Princeton: Princeton University Press.

Wagner, G. and M. Laublicher (2000). Character Identification in Evolutionary Biology: The role of the organism. *Theory in Biosciences*. 119: 20-40.

Wilson, J. (2021). Determinables and Determinates. *The Stanford Encyclopedia of Philosophy* (Spring 2021 Edition), E. Zalta, ed., URL = <a href="https://plato.stanford.edu/archives/spr2021/entries/determinate-determinables/">https://plato.stanford.edu/archives/spr2021/entries/determinate-determinables/</a>>.

Whitehead, H., K. Laland, L. Rendell, R. Thorogood, and A. Whiten (2019). The reach of geneculture co-evolution in animals. *Nature Communications* 10: 10293.

Whiten, A. (2019). Twenty questions about cultural gadgets. *Behavioral and Brain Sciences* 42, e169: 40-42.

Whiten, A. and D. Erdal (2012). The human socio-cognitive niche and its evolutionary origins. *Philosophical Transactions of the Royal Society B* 367: 2119-2129.