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CONCEPTS & SYNTHESIS

When the "satisficing" is the new "fittest": how a proscriptive definition of adaptation can change our view of cognition and culture

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Abstract
Since Darwin's theory of evolution, adaptationism is frequently invoked to explain cognition and cultural processes. Adaptationism can be described as a prescriptive view, as phenotypes that do not optimize fitness should not be selected by natural selection. From an epistemological perspective, the principle of a prescriptive definition of adaptation seems incompatible with recent advances in epigenetics, evolutionary developmental biology, ethology, and genomics. From these challenges, a proscriptive view of adaptation has emerged, postulating that phenotypes that are not deleterious will be evolutionary maintained. In this epistemological investigation, we examine how the shift from adaptationism to a proscriptive view changes our view of cognition and culture. We argue that, while adaptationism leads to cognitivism and a view of culture as strategies to optimize overall fitness, the proscriptive definition favors embodied theories of cognition and a view of culture as the cumulative diffusion of behaviors allowed by the constraints of reproduction.

Keywords Adaptationism · Neo-Darwinism · Neutral theory of evolution · Embodied cognition · Cumulative culture

"Nothing in biology makes sense except in the light of evolution" (Dobzhansky 1973). Seeing through the prism of evolutionary processes provides an empirical understanding of the diversity of life on Earth. In its broadest sense, natural selection predicts that differences in reproduction within a population of reproductive organisms are often due indirectly to differences in survival in a particular environment, leading to an increase in the proportion of beneficial, adapted, and heritable characteristics from one generation to the next (Darwin 1859). As such, Darwin gave us a framework for a theoretical interpretation of most phenomena we encounter in biology. Naturally, as this is a strong, integrative, and robust theory, its resulting predictions have been extended to human cognition and culture leading to many diverse frameworks (Dawkins 1976; Durham 1990; Wilson 2000; Tooby and Cosmides 2005) primarily (but not always) based on the assumptions of the neo-Darwinian synthesis. Indeed, according to the view of adaptation in the cognitive and social sciences, which we will call *adaptationism*, phenotypes are selected when they cope with the current environment most efficiently optimizing the odds of survival and reproduction (i.e., adaptative value). This view is *prescriptive*, as phenotypes that do not optimize adaptative value should not survive natural selection. According to this view, genes are the origin of phenotype when they are heritable (genecentrism) (see Meloni and Reynolds 2020). This prescriptive and gene-centered neo-Darwinian view has been challenged by recent advances in biology and genetics (Müller 2007; Danchin et al. 2019). Meanwhile, in cognitive sciences, adaptationism remains the predominant explanation for cognitive and cultural processes on the basis of their possible optimization of adaptative value (Durham 1990; Cosmides and Tooby 2013; Lacquaniti et al. 2013). In other words, according to the prescriptive view, cognition and culture are considered to be largely the result of a selection process that guarantees optimization of adaptive value.

Several limitations to the prescriptive view highlighted in biological sciences have led to alternative perspectives proposing a different definition of adaptation. This alternative view of adaptation is *proscriptive* (Varela et al. 1991), in the sense that phenotypes that are not incompatible with

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survival and reproduction are maintained. Although this proscriptive definition of adaptation is widely accepted in the biological sciences, it is rarely considered in the cognitive and social sciences to explain cultural and cognitive processes. Yet, the shift from a prescriptive definition to a proscriptive definition of adaptation in cognitive and social sciences could change our view of cognition and culture. In this essay, we propose a reflection on the adaptationist view and what it implies for cognition and culture, as it constitutes the dominant source of explanation of cultural and cognitive processes at present. Then, we consider the main criticisms that have been raised against it, leading consequently to new views on evolution, including a proscriptive definition of adaptation. Finally, we propose a reflection centered on this proscriptive definition and its implication for the evolutionary origins of cognitive and cultural processes and the resulting change in view of cognition and culture.

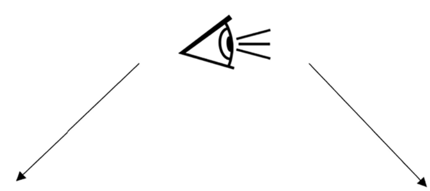
A *prescriptive* definition of adaptation and its implication for cognition and culture

The prescriptive definition is rooted in neo-Darwinism, a heritage of Darwin's theory, which can be summarized in three main assumptions: (1) evolution occurs as a gradual modification of organisms' phenotypes, propagated by heredity only if traits are inherited; (2) this hereditary material constantly undergoes diversification (through genetic drift and mutation); and (3) the genetically specified phenotypes that cope most efficiently with evolutionary pressures are naturally selected (Huxley 1942). This view is *prescriptive* as only the genes that determine traits optimizing the odds of survival and reproduction by their associated functions are selected. This prescriptive view has naturally led to consider that each organ in the body evolved to serve a specific function and is retained or discarded by natural selection depending on whether they optimally solve problems that affect global fitness/reproduction (Gregory 2008; Cosmides and Tooby 2013). Fitness should be understood here in its broadest sense, as the ability of organisms to survive and reproduce in the environment in which they find themselves (Orr 2009). Evolutionary psychology extended this assumption to the brain to explain its structure (Cosmides and Tooby 2013). According to this theory, the brain is composed of *modules* referring to separately modifiable, functional specializations sculpted by evolution (Barrett and Kurzban 2006). In this theory, the brain is then compared to a computer, i.e., a physical system processing information whose hardware (brain structure) and software (programs) were designed by natural selection (Fodor 1983). *Cognitivism* is the resulting predominant theory of cognition which considers cognition is based on mental representations: the mind is thought to computationally operate by manipulating symbols that represent features of the world or represent the world as being a certain way. According to the cognitivist approach, the core knowledge representations in cognition are amodal data structures processed independently of the brain's modal systems for perception and action and reside in a modular semantic system (Tulving and Murray 1985; Mandler 2002). Thus, cognitivism leads to two assumptions (among others): (1) sensorial perception is an input of information from a world with pregiven properties, and 2) representations are independent of modal (sensory) systems (Fodor 1983; Varela et al. 1991). We have previously seen in the context of an evolutionary interpretation of cognition that a prescriptive definition of adaptation leads to one of the core ideas of cognitivism, the modularity of cognition.

What about interpreting cultural processes in light of a prescriptive definition of adaptation? In *The Selfish Gene* (Dawkins 1976), Dawkins adds to neo-Darwinism the idea that genes are "selfish replicators" encoding phenotypes that increase their transmission to future generations, making organisms fundamentally "vehicles" for gene transmission. This gene-centered view of evolution implies that genes are relatively independent entities that specify phenotypes to enhance their own adaptative value. As a consequence, it has been proposed that different genetic elements either within an individual (intragenomic conflict) or between individuals (intergenomic conflict) have influence over the same phenotype, and an increase in transmission of one element by its phenotypic effects causes a decrease in transmission of the other (Werren 2011). When extended to human beings, this intergenomic conflict notion assumes that cultural behaviors are ways of increasing genetic transmission (e.g., male–female or sexual conflict, social roles, social conflict) (Rice and Holland 1997). The revival of Darwinism in social thinking was popularized with the emergence of sociobiology (Wilson 2000), i.e., the study of biological bases of animal behavior in the context of neo-Darwinian evolutionary theory, which has resulted in many studies and theories (Maxwell 1991; Nielsen 1994; Grafen 2003; Foster 2011). For instance, it was theorized that tickling entails a mock attack on vulnerable body spots and may provide youngsters with practice in defending themselves (Weisfeld 1993), that marriage and divorce can be understood as expressions of underlying gender-specific fitness maximization strategies (Buckle et al. 1996), and that sexual jealousy and the use or threat of male violence may serve genetic transmission (Daly et al. 1982). Another recent example of a prescriptive view of cultural processes, relevant to the COVID 19 pandemic, is the behavioral immune system (BIS) (Bacon and Corr 2020). BIS describes psychological and emotional responses to facilitate behavioral avoidance/escape from potential sources of infectious pathogens in the immediate environment (Schaller 2006). In humans, the emotion of "disgust" toward a social group, social categorization, and xenophobia have been described as manifestations of BIS to reduce the direct and indirect contact between an infected host and its healthy kin, improving inclusive fitness (Shakhar 2019). According to a prescriptive prism, cultural processes (e.g., social inequalities and discrimination) are thus considered as means to optimize global fitness (e.g., avoidance of infection). Taken together, according to a prescriptive definition of adaptation (adaptationism), the brain would be composed of modules sculpted by natural selection, while cultural processes would be strategies to maximize genetic transmission and increase adaptive value (Fig. 1).

The challenges of adaptationism

In *The Embodied Mind* (Varela et al. 1991), Varela raises several arguments against adaptationism which are supported by recent advances in several scientific disciplines such as epigenetics, evolutionary developmental biology (called evo–devo), cognitive neurosciences, and ethology. One of the main criticisms raised by Varela, among others (e.g., for a review, see Meloni and Reynolds 2020), against the adaptationist approach was its gene-centered view (where genes are independent and the only determinant of traits if inherited), as phylogeny (at the expense of ontogeny) was considered as the main causal source of phenotypic changes through heredity. Indeed, the standard modern synthesis framework neglected development which caused difficulties in explaining the origins of organismal form in mechanistic terms (Müller 2007). In response, the post-genomic approach moved the direction of research away from the naked gene to a broader consideration of the overall regulatory network of the genome (Moore et al. 2015). This wider architecture includes many *epigenetic* mechanisms involved in the regulation of gene expression during interaction with the environment (Cavalli and Heard 2019). Thus, epigenetics has the potential to explain aspects of phenotypic variability by reintroducing the role of development and environment (Henikoff and Greally 2016; Allis and Jenuwein 2016). Epigenetics is considered to be the primary underlying mechanism of *phenotypic plasticity*, i.e., the fact that genetically identical individuals may develop different phenotypes according to the environmental conditions in which they live (Schlichting and Wund 2014; Duncan et al. 2014). For example, phenotypic plasticity may not always facilitate genetic adaptation by bringing the organismal phenotype closer to the new optimum (Ho and Zhang 2018). Furthermore, evolutionary developmental biology research provides evidence that large morphological change is possible without necessarily requiring major genomic variations (Kampourakis and Minelli 2014) called saltational changes (Vogt 2017). Evolution is traditionally (since Darwin) viewed as proceeding in a countless number of very small steps, a view termed "gradualism." Yet, it seems that in some



	Prescriptive view	Proscriptive view
Definition	Selected if beneficial	Maintained if not detrimental
Prediction for the brain	Modules sculpted by adaptation through Natural Selection *Modularity of mind*	A hierarchically organized system of neurocognitive mechanisms *Predictive coding brain*
Prediction for Cognition	Based on mental representations of a preexisting world *Cognitivism*	Emerging, dynamic, embodied and situated *Embodied theory of cognition*
Prediction for Culture	Strategies to optimize global fitness	The cumulative diffusion of behaviors that survive the constraints of reproduction

Fig. 1 Epistemological differences between prescriptive and proscriptive views of adaptation

cases, profound saltational phenotypic changes may have occurred within one or a few generations of organisms (Theissen 2009). As this possibility is opposed to Darwin's own views (i.e., according to which evolution is a long gradual process) and to the prescriptive adaptationist perspective on evolution, for more than a century, it was hardly accepted (Bowler 2005). However, because of a better appreciation of the non-linear character of the genotype-to-phenotype map, saltational evolution is increasingly recognized (Kampourakis and Minelli 2014). For instance, saltational evolution has played an important role in understanding the evolution of functional innovations in non-specialized organisms (e.g., the case of snapping shrimp claws Kaji et al. 2018). Another important limitation to the adaptationist view is *pleiotropy*. Pleiotropy refers to the phenomenon of a single mutation or gene affecting multiple distinct phenotypic traits (Wang et al. 2010) which can have broad implications on adaptation. Indeed, pleiotropy seems to modulate the effect of selective pressures on phenotypic variation (Otto 2004). For instance, pleiotropic effects can reduce the efficacy of selection by limiting the fixation of beneficial mutations through adaptation and the removal of deleterious mutations (through purifying selection, see Fraïsse et al. 2019). Therefore, the genome is not a linear array of independent genes (manifesting as traits) but a highly interwoven network of multiple reciprocal effects (Solovieff et al. 2013). These limitations to the adaptationism view have led to ongoing debates centered on a rethinking of evolutionary theory (Baedke et al. 2020). From the reconsideration of evolution, new scientific disciplines emerged, such as the already mentioned evo–devo (the exploration of the mechanistic relationships between the processes of individual development and phenotypic change during evolution) (Müller 2007) and the neutral theory of molecular evolution (Guerrero-Bosagna 2017) which suggest that at the molecular level, evolutionary changes and polymorphisms within species are not caused by natural selection but by random genetic drift.

A *proscriptive* definition of adaptation and its implication for cognition and culture

Traditionally, explanations about the origin of evolutionary novelties are generally related to their adaptive value and are therefore based on ultimate causes. However, recent accumulating genomic evidence suggests that, beyond adaptive processes, nonadaptive processes are relevant in evolution supporting the neutral theory of molecular evolution (Kimura 1977). Indeed, epigenetically induced genetic variability could be produced independent of fitness effects or adaptive value (Guerrero-Bosagna 2017). All the mentioned weaknesses for adaptationism are compatible with a *proscriptive* definition of adaptation according to which, if variation arises and is not detrimental, it will be evolutionarily maintained. In this view, the evolutionary process operates by *satisficing* (taking a suboptimal solution that is satisfactory) rather than *optimizing* survival and reproduction. In other words, evolutionary processes are no longer a precise trajectory by the requirements of optimal fitness but rather the multiplicity of viable trajectories emerging through interaction with the environment. A consequence of this shift from "optimal selection" to "viability" is that the precision and specificity of morphological or physiological traits or cognitive capacities are *underdetermined* by the constraints of survival and reproduction while not being *specified* by it (Varela et al. 1991). The assumption that selection operates to satisfice viability rather than to optimize adaptive value is incompatible with the modularity of cognition invoked in evolutionary psychology, since the notion of "modules" is based on the idea that brain structures are associated with functions that have been selected to optimize adaptive value. Indeed, challenging the notion of "modules," recent advances in neuroscience provide evidence that epigenetics mechanisms occur at the neuronal level granting neurons a "reversible" reprogramming capability, allowing for plasticity at many levels (anatomical, electrical, synaptic…), called *neural plasticity* (Borrelli et al. 2008). Thus, in this view, the brain is no longer compared with a computer made of modules but rather is considered as a hierarchically organized system of neurocognitive mechanisms that interact in a dynamic, bidirectional fashion and that vary in the degree of functional specialization and integration (Badcock et al. 2019). As phenotypes emerge from interacting with the environment, neural dynamics depend heavily on the coupling between the organism and the environment suggesting that the body has a primary role in cognition (Meloni and Reynolds 2020). It is increasingly recognized that the body's physiological state underpins mental processes (Damasio and Carvalho 2013; Seth 2013; Pezzulo and Cisek 2016). Cognition is then embodied (rooted in the body) and situated (emerges from the interaction with the environment) operating by dynamic action–perception cycles. As such, perception does not come from pregiven proprieties of the world but emerges from interacting with it (Varela et al. 1991). This is consistent with the predictive coding brain framework which is gaining increasing traction within the cognitive and brain sciences (Seth 2013). It considers the brain as a constructive or predictive organ that actively generates predictions of its sensory inputs using prior experiences suggesting that predictions shape how we perceive and comprehend the world (Teufel and Fletcher 2020). A proscriptive definition of adaptation then favors embodied theories of cognition and dynamic hierarchical brain models.

The departure from a prescriptive definition means that cultural processes are no longer strategies to optimize (but rather satisfice) survival and reproduction. Epigenetic research suggests that lifestyle changes resulting from nutritional, toxicological exposures, and social and psychological changes are reflected in variations in the epigenetic profile of individuals correlating with learning and memory (Jablonka 2016). Thus, interacting with a complex structured social environment can influence gene expression and even cognition. Culture can be one of many influences that shape behavior (Brakes et al. 2021) and could have the potential to affect evolutionary processes in several ways (e.g., social learning and cultural innovations) (Beans 2017; Whiten 2021). According to a proscriptive view, cultural processes could thus be the result of the coupling between an organism and its environment (including the social aspects) as emerging viable trajectories underdetermined by the constraints of survival and reproduction, possibly influencing evolution processes rapidly due to its cumulative nature (Whiten 2019).

The relevance of a proscriptive definition of cultural processes is highlighted by the influence of cultural innovations on evolutionary trajectories, which do not always optimize adaptive value yet are compatible with survival and reproduction. To illustrate this, we take the example of niche construction. Niche construction is the process whereby organisms, through their activities and choices, modify their own and each other's niches (immediate environment) consequently transforming natural selection pressures. Niche-constructing species play important ecological roles by creating habitats and resources used by other species and thereby affecting the flow of energy and matter through "ecosystem engineering" (Laland et al. 2016). A representative example of engineer organisms is fossorial mammals which, by changing the geomorphology, gained new morphological, biomechanical, physiological, and behavioral feedback traits for living in burrows and changed the evolutionary feedback at the ecosystem level (Corenblit et al. 2021). Niche construction is particularly relevant to cultural practices as they involve extensive environmental modifications (Laland and O'Brien 2011). For instance, Lactase is the enzyme responsible for the digestion of lactose and its production decreases after the weaning phase in most mammals, including humans. Some humans, however, due to cultural niche construction, continue to produce lactase throughout adulthood, a trait known as lactase persistence (Gerbault et al. 2011). Another example would be human behavior in response to temperature fluctuations, such as putting on and taking off clothes, building fire, and developing cooling systems, which tends to negate these temperature-related selection pressures (Laland and Brown 2006). In the same way, cultural innovations might exert epigenetics changes (Jablonka 2016). For instance, Jablonka takes the example of the reconstruction of poverty which emerged from many factors such as developmental effects of malnutrition; the consumption of unhealthy food, alcohol, or other toxins; poor education; and limited job opportunities (Jablonka 2016). Those factors sustaining the trajectories that lead to poverty are correlated with an increased risk of cardiovascular diseases, cancer, and psychological disorders, which all have epigenetic underpinnings (Thayer and Kuzawa 2011; Lock 2015). In this feedback loop, the social system and the epigenetic landscape are in reciprocal interactions (Jablonka 2016). Another example could be the act of colonization (based on cultural innovations such as building ships) which leads to favoring adipose tissue increasing survival odds during long travels with scarce resources (O'Rourke 2014). Yet, this metabolic thrift favoring obesity in our modern societies has been maintained despite not optimizing adaptative value while not being incompatible with survival and reproduction. In those examples, cultural consequences (e.g., obesity and poverty) are more likely to emerge as satisfactory viable trajectories (not detrimental to global fitness) than being selected for their adaptative value. Moreover, contrary to the prescriptive view which suggests a certain degree of inevitability as they are selected, the proscriptive approach predicts that cultural practices are flexible offering relevant experimental leads in social sciences. As such, we propose a proscriptive view of culture which can be defined as the cumulative diffusion and transmission of behavior through social learning (the consensual definition in ethology (Whiten 2019)) that satisfies general fitness constrains (Fig. 1). This definition encapsulates the complexity and diversity of cultural practices and reintroduces the role of culture as a source of influence in shaping behavior. This definition of culture accounts for the notion of "epigenetic landscape," i.e., a metaphoric platform by which multiple environmental factors interact with complex genetic information, resulting in modifications in gene expression that shape cellular and neuronal functions, ultimately directing the specification of individual diversity (Waddington 2014; Jablonka 2016).

Conclusion and outlook

In this epistemological inquiry, we considered the implications of a proscriptive definition of adaptation (i.e., phenotypes that are not detrimental will be evolutionarily maintained) for cognition and culture. In a proscriptive context, natural selection can be seen to operate not by selecting phenotypes that optimize adaptation value but rather by discarding phenotypic and genotypic variants constrained by survival and reproduction. We suggest that a prescriptive definition of adaptation (i.e., phenotypes that do not optimize adaptative value should not be selected by natural selection) leads to a view of the brain as composed of modules sculpted by natural selection and cultural processes as strategies to maximize genetic transmission enhancing adaptative value. In contrast, a proscriptive perspective favors a view in which the brain is a hierarchically dynamic organized system of neurocognitive mechanisms, and cognition emerges from the coupling with an environment. In the same way, cultural processes are viable evolutionary trajectories constrained (but not specified) by survival and reproduction which are characterized by the transmission and diffusion of behaviors through social learning. From an epistemological standpoint, the tenet of a prescriptive definition of adaptation appears incompatible with recent advances in epigenetics, evolutionary developmental biology, ethology, and genomics. This new empirical evidence becomes a source of explanation for a proscriptive viewpoint as it highlights the enormous diversity constantly generated at all levels in the genetic and evolutionary processes that both shape and are shaped by the coupling with an environment. The growing empirical support for the proscriptive view was previously discussed by Guerrero-Bosagna (2017) who concluded that the main path taken by evolution might not be "the survival of the fittest" but rather "the survival of the nonunfit." We added weight to this perspective by extending the epistemological importance of a proscriptive definition to the explanation of cognition and culture through a holistic consideration of biological, cognitive, and cultural levels. We proposed that, according to a proscriptive view, (1) culture is the cumulative diffusion and transmission of behavior through social learning that *satisfies* general fitness constraints, and (2) cognitive processes emerge from the coupling between the organism and its environment as long as they *satisfy* viability. Although the proscriptive views of culture and cognition are supported by recent empirical evidence, neither is dominant in the cognitive and social sciences. Yet, "the survival of the satisficing" may be the primary pathway for evolution that, when considered, changes our view of cultural and cognitive processes. Indeed, this proscriptive view of adaptation offers the possibility to make strong predictions at the biological, cognitive, and cultural levels. This alternative research program can provide great epistemological fecundity and should be more investigated not only in biological sciences but in other scientific disciplines, as well as social and cognitive sciences, in which adaptationism is still the main theory invoked to explain observed phenomena.

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Declarations

Competing interests The authors declare no competing interests.

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