Biological Theory
https://doi.org/10.1007/s13752-024-00468-2

ORIGINAL ARTICLE

Mismatch Resistance and the Problem of Evolutionary Novelty

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Received: 28 October 2023 / Accepted: 5 June 2024

Abstract
In evolutionary medicine and other related fields, the concept of evolutionary mismatch is used to explain phenomena whereby traits reduce in adaptive value and eventually become maladaptive as the environment changes. This article argues that there is a similar problem of persistent adaptivity—what has been called the problem of evolutionary novelty—and it introduces the concept of *mismatch resistance* in order to explain phenomena whereby traits retain their adaptive value in novel environments that are radically different from the organisms' environment of evolutionary adaptedness (EEA). The possible role of variability selection in the evolution of mismatch-resistant traits is discussed, and it is suggested that mismatch resistance provides a useful tool for making progress on certain issues related to evolutionary theory, such as the modularity debate, cases of adaptivity outside of organisms' ancestral environment, and the viability of naturalism as an overarching philosophical framework for understanding the natural world.

Keywords Evolutionary mismatch · Evolutionary novelty · Mismatch resistance · Modularity · Scientific explanation · Variability selection

Introduction

Natural selection is a temporal process influencing the evolution of biological organisms with radically different relationships to past and future conditions of life. It has been described as being "blind to the future and [with] no long-term goal" (Dawkins 1996, p. 50), as a process that is not teleological or forward-looking, and that any adaptation it produces necessarily must be to environmental conditions experienced in the ancestral past (Gregory 2009, p. 163). As lucidly argued in *On the Origin of Species*, phenotypic adaptations are produced by a natural process that selects among inheritable variants that prove beneficial in the "struggle for life." As Darwin put it:

> Owing to this struggle for life, any variation, however slight and from whatever cause proceeding, if it be in any degree profitable to an individual of any species, in its infinitely complex relations to other organic beings and to external nature, will tend to the preservation of that individual, and will generally be inherited by its offspring. […] I have called this principle, by which each slight variation, if useful, is preserved, by the term Natural Selection. (Darwin 1859, p. 61)

However, the claim that adaptations are produced by a process of selection among inheritable variants seemingly conflicts with the observation that some traits appear to be adapted to novel environmental conditions. Darwin (1871, p. 158) himself remarked upon "[man's] great power of adapting his habits to new conditions of life," noting that "he invents weapons, tools, and various stratagems to procure food and to defend himself," that "he uses clothes, builds sheds, and makes fires," and that he in myriad other ways "anticipates future events" in a manner that clearly is adaptive. But how can it be that certain traits are highly adaptive in novel environments that are *fundamentally different* from those in which selection initially favored the traits? There may not appear to be any reason as to why what proves to be a functional variant in one environment should also be functional in some other environment that involves other selection pressures and other adaptive problems that the organism must overcome to be reproductively successful; yet, as Darwin's remark in *The Descent of Man* (1871) illustrates, selection has produced such traits, including the behavioral

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flexibility that has enabled humans to adaptively anticipate "future events" and thrive under "new conditions of life." This apparent conflict between selection as a process that is "blind to the future" and the fact that many traits are adaptive under novel environmental conditions has been termed *the problem of evolutionary novelty* (Chiappe and Gardner 2012, p. 679; Sterelny 2012).

The problem of evolutionary novelty lies at the heart of a number of contested issues related to evolutionary theory, some of which are found in the evolutionarily informed sciences, such as evolutionary psychology and biology, and others which belong to more distally related disciplines, such as philosophy. These issues include the modularity debate, adaptivity outside of organisms' ancestral environments, and the viability of naturalism as an overarching framework for understanding the natural world and the various spatiotemporal entities existing therein. In order to attempt to make some progress on these issues, this article will argue that the literature on evolutionary mismatch, as well as recent work on the effects of variability selection, can, when properly synthesized, offer a solution to the problem of evolutionary novelty. By offering such a synthesis, the concept of *mismatch resistance* will be introduced, and it will be argued that it provides a useful tool for moving the debates surrounding the aforementioned issues forward.

Evolutionary Mismatch: A Conceptual Analysis

The concept of evolutionary mismatch was developed to explain how traits can go from being adaptive to being maladaptive as the environmental conditions that the population is exposed to change. Versions of this phenomenon, where a population is unable to deal with rapid environmental changes and therefore faces extinction, were described early on by Mayr (1942, pp. 224–225) as "evolutionary traps." Another term used to cast light on the same phenomenon is "adaptive lag," which occurs when the adaptive value of a trait declines due to relatively rapid environmental changes—i.e., environmental changes occurring at a rate which causes traits to lose some of their previous adaptive value under the current selection pressures (Eaton et al. 1988; Laland and Brown 2006). The concept of evolutionary mismatch has also been used in the burgeoning field of evolutionary medicine—highlighting possible pathological effects of the phenomenon (Williams and Nesse 1991; Nesse and Williams 1998; Kennair et al. 2018)—and a taxonomy has started to develop surrounding the different ways in which conditions of mismatch can occur as a consequence of adaptive lag (Gluckman et al. 2009; Bourrat and Griffiths 2024). According to one literature review,

> The central premises [of evolutionary medicine] are straightforward: (1) Our gene pool was shaped by natural selection for optimal function in past environments […] (2) [M]ost of our genome remains adapted for ancestral conditions. (3) The resulting mismatch between our ancient bodies and the circumstances of modern life in affluent Western nations fosters development of chronic degenerative diseases. (Eaton et al. 2002, p. 110)

However, getting at a precise definition of evolutionary mismatch has proved somewhat difficult. Consider the following three definitions recently introduced in the literature:

> This paper defines mismatch as *deviations in the environment that render biological traits unable, or impaired in their ability, to produce their selected effects* (i.e., to perform their proper functions[)]. (Cofnas 2016, p. 508)
>
> Evolutionary mismatch obtains when an organism O is in an actual environment E_a such that O's fitness is lower than it would be in an optimal environment E_{mf}. (Morris 2020, p. 4031)
>
> Mismatch requires a phenotype in an environment and another reference environment in which the phenotype does better than in its actual environment. It also requires a currency, which is usually biological fitness. (Griffiths and Bourrat 2023, p. 280; cf. Bourrat and Griffiths 2024)

None of these definitions seems to be without problems or limitations. According to Cofnas, mismatch occurs when environmental change makes a trait not perform its proper function (i.e., its selected effects). However, this definition is clearly at odds with the common view in evolutionary medicine that the concept of evolutionary mismatch has to do with environmentally induced reductions in the adaptive value of a trait. Moreover, whereas this common view clearly renders the concept of mismatch useful, in the sense that it helps explain various phenomena in which the adaptive values of certain traits lag, it is not clear what explanatory value the concept has on Cofnas's view. How, for example, does it explain the effects of adaptations that have become maladaptive? This problem is largely symptomatic of the fact that a trait's function (which he understands in terms of "the effect(s) of the trait that it was selected for—the effects that played a causal role in its selection"; Cofnas 2016, p. 510) and its adaptive value can come apart. The mechanisms underlying our preferences for sweet and salty foods might very well perform their evolved proper functions, even though they are in a state of mismatch with respect to current environments of abundant and easily accessible sweet and salty foodstuffs. Similarly, one can imagine a scenario where the same mechanisms are not performing their proper functions, but they nevertheless don't exist in a state of mismatch—perhaps the reason they aren't mismatched is *because* they are not performing their evolved proper functions, which, under current selection pressures, would result in maladaptive outcomes. An example of this could be that there is a drug that downregulates our preferences for sweet and salty foods, which would mean that the preferences are not mismatched precisely because they are not (due to the effects of the drug) performing their proper functions.

Morris's definition of evolutionary mismatch, which compares an organism's fitness in the actual environment with its fitness in an optimal environment, is also problematic. This definition is also inconsistent with how the concept is used in evolutionary medicine, and, furthermore, it is not clear that the concept retains its explanatory value. The reason is that the optimal environment, according to Morris (2020), "is the environment in which the organism's fitness is maximized: in other words, the optimal environment is that in which the organism's fitness is as high as it can possibly be." But if evolutionary mismatch is understood with reference to the optimal environment in this manner, it follows that all organisms exist in a state of mismatch. And if that is true, then the concept cannot be used to explain phenomena of reductions in adaptive value due to adaptive lag—i.e., cases of relatively worse fitness outcomes under current selection pressures compared to ancestral ones. An argument could of course be made that Morris wants to develop an alternative notion of mismatch, but one would then have to motivate why this new conception is explanatorily superior to the conception that already is established in, for example, evolutionary medicine and psychology.

Lastly, the definition of Griffiths and Bourrat, which compares an organism's fitness in the actual environment with its fitness in a reference environment, gives an adequate analysis of mismatch, given that the concept is understood in terms of *relative maladaptation*, which has to do with an individual or population having lower fitness than some other individual or population, rather than *absolute maladaptation*, which means sub-replacement fitness ($W < 1$) (Brady et al. 2019). They note that the reference environment is typically understood in terms of Bowlby's (1969) "environment of evolutionary adaptedness" (EEA), which is the set of environmental selection pressures that historically has influenced an adaptation (Bennett 2018). This means that an organism is in a state of mismatch with respect to a particular trait when the fitness outcomes of the trait are worse in the actual environment than in the ancestral environment that it is adapted to. However, there are a couple of reasons why their analysis ought to be supplemented. The first is that it would also be valuable to have an analysis of mismatch that focuses on absolute maladaptation, since absolute maladaptation is an evolutionary phenomenon that is interesting in and of itself. The second, and related, reason is that this latter kind of analysis would enable us to explain why traits that are highly adaptive need not be classified as mismatched, even though their adaptive value in the actual environment is lower than in the EEA. To illustrate such a case, imagine a trait with enormously positive fitness consequences in the actual environment, and with marginally better fitness effects in the EEA. Intuitively, there is a sense in which this clearly is not a mismatched trait, and that sense would be captured by an analysis of mismatch that is cashed out in terms of absolute, rather than relative, maladaptation.

In light of the aforementioned problems and issues, an alternative analysis of the concept of evolutionary mismatch can be developed, according to which mismatch occurs when a trait has gone from being adaptive in the ancestral environment (or EEA) to being (absolutely) maladaptive in the actual environment (Box 1). More specifically, an individual *i* with a phenotypic trait of interest is mismatched in the actual environment *AE* when compared to the *EEA* for the fitness function *W*, if $W_{i,AE} < 1$, and $W_{i,EEA} > 1$.[1] This simple formula satisfies two important desiderata for any adequate analysis of evolutionary mismatch: (1) consistency with current usage in evolutionary medicine (and other fields, such as psychology); and (2) it must account for cases of adaptive lag experienced in the actual environment compared to the ancestral environment in which the trait evolved, which result in maladaptation. Evolutionary mismatch (in the absolute sense of the term) occurs whenever a trait negatively contributes to fitness in the individual's actual environment, even though it used to have a positive relationship with fitness in the EEA.

Box 1: A schema for evolutionary mismatch, with explanations of relevant terms

i An individual with a phenotypic trait of interest
AE The actual environment of an individual
EEA The environment of evolutionary adaptedness; i.e., the environment(s) in which a particular trait of an individual evolved
W The fitness function

Evolutionary mismatch (in the absolute sense of the term) can then be described as a phenomenon that occurs if the following two conditions obtain:

$W_{i,AE} < 1$
and
$W_{i,EEA} > 1$

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[1] For simplicity, it is assumed that reproduction is asexual. The analysis can easily be extended and made to account for cases involving sexual reproduction.

Mismatch Resistance: When Adaptation Does Not Lag

If evolutionary mismatch occurs as a trait transitions from being adaptive to being maladaptive, then a trait can be said to be *mismatch resistant* when it is not particularly vulnerable to that kind of environmentally induced adaptive lag. Mismatch resistance can, in other words, be said to characterize phenotypic traits that, for whatever reason, are relatively unlikely to function as a source of evolutionary mismatch as organisms gradually become more removed from the ancestral conditions that the traits in question are adapted to. There are, furthermore, three important points that should be stressed as this novel concept is discussed.

Just as traits can be more or less mismatched in terms of their fitness outcomes when comparing the actual environment and the ancestral environment, traits can also be more or less mismatch resistant. That is just to say that mismatch resistance is a continuous variable, and that no a priori assumption can be made about the precise degree to which a certain trait of interest is resistant or insusceptible to environmentally induced adaptive lag.

In order for a trait to qualify as mismatch resistant, it is neither necessary nor sufficient that its fitness consequences in the actual environment are not negative. Rather, what is required is that its fitness consequences are not negative, or that it is not maladaptive, in the frequency-weighted sum of environments experienced by the population in which it has occurred since its evolution in the EEA. In other words, it is not enough that the trait doesn't exist in a state of mismatch in the actual environment as it is right now; it must have proved useful—or at least not maladaptive—since its evolution in the EEA.

That a trait is mismatch resistant does not in any way guarantee that it will not become maladaptive and, hence, a source of evolutionary mismatch in the future. Mismatch resistance is in this sense also a "backward-looking" concept. However, since mismatch resistance implies past evolutionary success, often over extended time periods, the application of the concept to a trait does offer inductive support to the idea that the trait also might be beneficial in future environments.

This last point is important since it hints at a possible solution to the problem of evolutionary novelty. Recall that the problem is not that we have phenotypic adaptations to novelty per se. That cannot be the case, since "adaptation is impossible without *some* environmental signal" (Barrett and Kurzban 2012, p. 686; emphasis in original); which is to say there cannot be adaptation to an environment that the organism's ancestors did not experience. Rather, the problem is to explain how our evolved traits can respond to many kinds of novelty in an adaptive way—how there can be mechanisms that increase the probability of coming up with solutions to new problems—even though adaptation to novelty as such is impossible. Just as maladaptation in the actual environment presents an explanatory challenge, so does adaptation in novel environments that are fundamentally different from the EEA. The central suggestion of this article is that evolutionary mismatch resistance is to the latter challenge what evolutionary mismatch is to the former.

Having introduced the concept of mismatch resistance, the rest of this article will argue that mismatch-resistant traits likely will be favored by certain kinds of selection pressure, and that the concept can be used to make progress on certain seemingly intractable problems related to evolutionary theory.

Variability Selection and Mismatch-Resistant Adaptations

Among evolutionary psychologists, a common idea is that only (or primarily) invariant features of the environment that intergenerationally recur can constitute selection pressures that have shaped our present adaptations.

> This functional organization in the organism—its set of adaptations—is designed to exploit the enduring properties of the environment in which it evolved (termed its environment of evolutionary adaptedness, or EEA) and to solve the recurring problems posed by that environment. […] As adaptations, they themselves have complex structures that assume and require recurrent features of the world, and that interact with this recurrent structure to produce biologically functional targeted outcomes. (Tooby and Cosmides 1992, pp. 69, 77; cf. Tooby and Cosmides 1995)
> In particular, evolutionary psychologists constrain themselves to positing only biological mechanisms for dealing with inputs that would in principle have been recurrent over evolutionary time (and therefore cannot propose mechanisms that take as inputs evolutionary novelties, unless these inputs are taken in as a side effect or by-product of the mechanism's evolved structure[)]. (Pietraszewski and Wertz 2022, p. 477)

If this is true, then it is hard to see how natural or sexual selection can favor the evolution of mismatch-resistant traits. For if adaptations function to produce adaptive outcomes only when they interact with environmental features that recurred in the EEA, then there is no reason to think that they will lead to similar outcomes when the environment changes. As Pietraszewski and Wertz note, any operation performed by a phenotypic mechanism in a novel environment must be considered a by-product or, to use Gould and Lewontin's (1979) term, a *spandrel*.

However, as, for example, Geary and Huffman (2002, p. 679) note, selection pressures (whether natural or sexual) are generally characterized by both relatively variant and relatively invariant aspects. And whereas invariant patterns, such as universal features of the human face, are expected to favor quick and inflexible adaptations, those that involve a high degree of variability, such as complex social dynamics, are likely to favor adaptations that are more plastic and open to experiential modification. When interrelationships between organisms play an important role in determining fitness outcomes—which crucially happens in host–parasite (Hamilton and Zuk 1982) and predator–prey dynamics (Dawkins et al. 1979)—such outcomes should be better for organisms with facultative traits that involve some degree of unpredictability (Maynard Smith and Price 1973). A good example is the coevolutionary arms races that are known to occur between hosts' immune-system defenses and parasites' defense-evasion mechanisms (Van Valen 1973; Hamilton et al. 1990). The hosts' immune systems randomly produce a variety of antibodies, and those that are successful at combating invading parasites are selected. On the parasite side there is also a variety of defense-evasion mechanisms, and those that are effective at avoiding or neutralizing the hosts' defenses are selected. The reason why this arms race in principle can go on indefinitely is that the immune system is adapted to this kind of variability and, as a result, reliably produces facultative and (from the point of view of the parasites) unpredictable responses.

Potts (1998) has referred to adaptations produced by variable and inconsistent selection pressures as *variability selection*, arguing that they are likely to exhibit a kind of adaptive flexibility that proves beneficial in a range of different ecologies (cf. Potts 2013). This coheres with Vrba's (1988) argument that generalist species are much less likely to experience extinction events than specialist species, since generalists are better at utilizing new environmental conditions. Moreover, there are reasons for thinking that variability selection provides an essential tool for understanding hominin evolution. All the major events in the evolution of the hominin line occurred in East Africa, with much of the action happening in the East Africa rift system (Dartnell 2019). The literature review by Maslin et al. (2014) provides strong evidence that the extreme geological and climatic variability of the East African landscape over the last 10 million years has played an important role in hominin speciation and dispersal out of Africa (cf. Loulergue et al. 2008; Mercader et al. 2021; Foister et al. 2023), and plausibly also in the evolution of larger brains and increased cognitive ability (Sterelny 2003; Richerson and Boyd 2000).

As more data are gathered and analyzed, variability selection increasingly seems like a plausible candidate for explaining not just what makes our human species so special, but also why so many other organisms thrive under diverse environmental conditions—even though it is sometimes presented using different terminology. Godfrey-Smith (2002), for example, argues that the evolved function of cognition (in both human and nonhuman animals) is to enable the organism to deal with environmental complexity. However, complexity, we're told, is just another word for "heterogeneity," "variety," and "diversity." Moreover, Godfrey-Smith (2002) aptly notes that environmental complexity should not just be seen as posing problems that organisms must overcome to pass on their genes; it also presents opportunities. Variable environments may present "adaptive opportunities" that organisms can take advantage of, but only if their traits are flexible and open to experiential modification. Organisms whose traits are less flexible or plastic might, on the other hand, be "blind" to these opportunities.

Given the assumption that only intergenerationally recurrent patterns of invariant environmental information can constitute selection pressures, we should expect all adaptations to be highly specialized in their evolved functions. When it comes to behavioral evolution, we should similarly expect the information processing that goes on in human and nonhuman brains to be dominated by highly specialized cognitive mechanisms that only take as inputs and operate on information from narrow content domains—or in other words, it should be dominated by "instincts" (cf. Cosmides and Tooby 1992; Buss 2020). However, if instead variability selection provides a plausible explanation for the evolution of adaptive flexibility, then we should expect such selection pressures to favor adaptations that are less likely to be vulnerable to adaptive lag that results in evolutionary mismatch. More specifically, we should expect a subset of human and nonhuman adaptations to be mismatch resistant, in the sense that they are likely to retain (some of) their adaptive value even under novel environmental conditions. The *mismatch-resistance hypothesis*, which claims that some adaptations are mismatch resistant, is supported by recent work on variability selection, and also by the fact that it offers a plausible solution to the problem of evolutionary novelty. If some variability-selected traits are mismatch resistant, then we would predict that those adaptations should be likely to retain some of their functional, adaptive value, even in novel environments that involve other selection pressures and other adaptive problems.

Here, the very general mismatch-resistance hypothesis is presented primarily to demonstrate that it solves certain contentious issues related to evolutionary theory—the most important of which is the problem of evolutionary novelty. It does not hypothesize that any specific trait is a mismatch-resistant adaptation. However, the next sections will argue that the hypothesis under consideration has important implications for the modularity debate in evolutionary psychology, the so-called "Savanna Principle," and even for our understanding of naturalism as an overarching philosophical framework for understanding the natural world.

The Modularity Debate

There are different ways of understanding the notion of modularity, most of which reference a subset of the properties invoked by Fodor (1983) in his seminal discussion. Fodor argued that prototypical modular systems, like input systems involving perception and language, are a *natural kind*—i.e., a grouping of certain particulars that reflects that actual structure of the natural world—since they necessarily are *informationally encapsulated* (Fodor 1983, pp. 71, 98–99). Information encapsulation means that there is a restriction on the flow of information into a certain system; that there is information contained elsewhere in the "belief system" that modules cannot access. Although the Fodorian conception of modularity has been highly influential, most of the discussion surrounding modularity today, especially in evolutionary psychology, focuses on another property that Fodor also associates with modules—namely, *domain specificity* (Egeland 2023, 2024; Villena 2023). A cognitive system is domain specific if the information it takes as inputs and operates on comes from some narrow and specific content domain. According to Fodor (1983, p. 103), "domain-specificity has to do with the range of questions for which a device provides answers (the range of inputs for which it computes analyses)."

Now, the dominant position in evolutionary psychology has for quite some time been that all (or most) cognitive mechanisms must be modular, in the sense that they are domain specific, since selection pressures are assumed to be constituted by intergenerationally recurrent and invariant features of the environment (Tooby and Cosmides 1992, p. 110). In fact, one often finds that the claim that the mind must be massively modular in its structural organization is directly inferred from the assumption that all (or most) selection pressures come in the form of invariant features of the environment (e.g., Tooby and Cosmides 1992, pp. 69ff.; Bjorklund and Blasi 2015; Boyer and Barrett 2015), or, even more ambitiously, that it is directly inferred from basic Darwinian theory. An example of the latter strategy is found in the work of Pietraszewski and Wertz, who argue that the massive modularity thesis is both "boringly axiomatic" and "simply a logical entailment of Darwin's theory of natural selection" (2022, p. 478). However, Egeland (2024) has recently shown that the thesis that the mind's organization is massively modular is not an entailment of Darwinian theory, and that it cannot be considered as "axiomatic" without begging the question, since that would be to assume the correctness of one's conclusion, rather than providing reasons supporting it. Moreover, there are also multiple lines of evidence indicating that variable features of the environment will influence the selection of inheritable traits, and that under conditions of variability selection cognitive mechanisms that are adaptively flexible, and that typically involve slow, effortful, and explicit processing, will be favored (Richerson and Boyd 2000; Chiappe and MacDonald 2005; Geary 2005, Chap. 6; 2007; Chiappe and Gardner 2012; Burkart et al. 2017).

Given that variable and complex environmental conditions tend to select for mismatch-resistant traits, and that such conditions have characterized much of our evolutionary history, a natural question becomes what mismatch-resistant cognitive adaptations would have to look like. In other words, in virtue of what properties may a cognitive mechanism be mismatch resistant? One property that plausibly is conducive to cognitive and behavioral mismatch resistance is *domain generality*—i.e., that the mechanism functions to take as inputs and to operate on information from broad content domains. Moreover, in contrast to previous ideas to the effect that there are no domain-general psychological traits, such traits are just one example of the broader category of *phenotypic plasticity*—referring to phenotypic mechanisms with reaction norms that are sensitive to a range of different environments (Whitman and Agrawal 2009; Fawcett et al. 2013; Kolodny et al. 2015; Tomasello 2022; Baumard et al. 2023). Of course, properties of domain specificity and domain generality exist on a continuum, and saying that a cognitive mechanism is domain general does not imply that it must function to adaptively process any kind of information, or that it would serve the general purpose of promoting gene replication. The latter idea represents an unsupported and outdated manner of understanding adaptive evolution (Symons 1992), and the claim that some of our cognitive mechanisms may be mismatch resistant emphatically does not imply a commitment to it.[2]

However, this claim indicates that our cognitive and behavioral repertoire is much richer and more diverse than what initially has been suggested and may therefore provide

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[2] There can be no such thing as a maximally general or specific cognitive system, as both positions are vulnerable to *reductios*. General systems are relatively weak, and any such system must rely on algorithms for processing incoming information and evaluating its significance; on the other hand, if the cognitive systems are maximally specific and designed only to deal with a problem space of narrow granularity, then the systems should produce entirely random behavioral outputs when the environment changes. The balance between general and specific systems will always be a function of evolutionary trade-offs.

grounds for unifying contemporary evolutionary psychology with other subfields that historically have relied on somewhat different theoretical assumptions about the human mind, such as human behavioral ecology and cultural evolution (cf. Brown and Richerson 2014). Rather than conceiving of the mind as being massively modular and as more or less exclusively being furnished with a great many "instincts" that allow for fast and efficient decision-making based on genetically encoded behavioral heuristics, it suggests that such modular systems exist alongside more operationally complex and adaptively flexible systems. This position also coheres with emerging empirical evidence indicating that the latter kind of cognitive system indeed does contribute to adaptive behavior in many different animal species, that some of these systems are homologous across much of the animal kingdom, and that the human brain is not modularly organized (Bitterman 2000; Bolhuis and Macphail 2001; Kane and Engle 2002; Lefebvre and Bolhuis 2003; Geary 2007, 2009; Bolhuis et al. 2011; Reader et al. 2011; Elimari and Lafargue 2020; Holyoak and Monti 2021; Roy et al. 2022; Wang et al. 2022).

Moreover, the concept of mismatch resistance may enable us to provide explanations of certain traits that earlier evolutionary analyses have not been able to integrate. Consider, for example, honest signals whose evolved function is to alter the behavior of the recipient in a way that benefits the signaler by somehow reliably conveying useful information about some unobservable factor (Wiley 2013). Such evolved traits, sometimes called fitness-indicators in evolutionary psychology, generally don't satisfy the typical adaptationist criteria: rather than having properties such as modularity, low heritability, low phenotypic variance, and low genotypic variance, such traits often have opposite properties—which suggests that the standard view of adaptation in evolutionary psychology ought to be expanded (Miller 2000a, b). Now, the concept of mismatch resistance may provide grounds for such an expansion, since honest signals likely will be beneficial in a range of different environments as long as their signaling function is reliable and provides useful and discriminable information to receivers, and there is some evidence that they become more reliable indicators of underlying quality when environmental stressors increase (Candolin and Voigt 2001), which often happens under novel ecological conditions. Furthermore, another property of such traits is that they may tend to be more evolvable by virtue of their relatively high levels of heritable variance, and this also means that they are somewhat unlikely to function as a source of adaptive lag as organisms become more removed from the EEA. Mismatch resistance functions as a broad conceptual category of adaptation, allowing for the inclusion of traits that sometimes escaped earlier evolutionary analyses, including psychological traits that are known to have properties such as non-modularity, moderate/high heritability, moderate/high phenotypic variance, and moderate/high genotypic variance (cf. Miller 2000a, b).

The general mismatch-resistance hypothesis thus suggests that there need not be any tension or conflict between modular and domain-general systems, but rather that both are necessary for organisms to deal with relatively invariant and variant aspects of the environment, respectively.[3]

Life away from the Savanna

To what extent should we expect human cognition and behavior to be adaptive outside of our ancestral environment (or EEA)? Evolutionary psychology recognizes that getting an adequate understanding of our evolved human psychology requires some insight into the various adaptive problems that had to be overcome for our Pleistocene ancestors on the African savanna. The fact that all humans appear to have evolved the same psychological mechanisms, which means that there is in some sense a universal human nature, provides strong evidence that our psychology and behavior largely is adapted to life on the African savanna (Tooby and Cosmides 1990). However, since adaptivity in one environment does not logically imply either adaptivity or its opposite in another environment, this leaves unanswered the question of how adaptive we should expect human psychology and behavior to be away from our environment of evolutionary adaptedness.

To answer this, Kanazawa (2004, p. 43) has proposed what he calls the *Savanna Principle*, which says that the human brain should struggle to adaptively deal with environmental conditions that are different from those of the African savanna during the Pleistocene (cf. the evolutionary legacy hypothesis by Burnham and Johnson 2005, pp. 130–131; and the mismatch hypothesis by Hagen and Hammerstein 2006, pp. 341–343). The Savanna Principle can be used to explain different ways in which human behavior is mismatched to our current environments relative to the EEA, and how this mismatch may result in, for example, irrational decision making and chronic disease. However, it cannot explain the fact that humans have undergone massive adaptive radiation during the Holocene (Hawks et al. 2008; Brown and Richerson 2014). Moreover, humans apparently possess some cognitive and behavioral traits that make them able to handle certain parameters of

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[3] By offering a way of making sense of the evolution of domain-general cognitive mechanisms, the mismatch-resistance hypothesis stands in stark contrast to the idea that adaptive evolution cannot explain the human mind or its more peculiar cognitive mechanisms (cf. Fodor 2002).

environmental novelty remarkably well. Most humans are able to acquire nutritious foods from supermarkets, while making sure that they are maintaining a budget. Or think about the enormous progress that has been made in the sciences during the past couple of centuries: using our evolved cognitive mechanisms for reasoning in conjunction with inputs from our senses, we have figured out what the speed of light is, and that it always is the same in a vacuum; we know what the molecular structure of DNA is and how to edit it using naturally evolved sequences of clustered regularly interspaced short palindromic repeats; and we know that the appearance of design in nature can be explained as a natural consequence of chance and selection influencing populations of organisms.

It is not just phenomena of adaptive lag leading to evolutionary mismatch that call for an explanation, but also phenomena having to do with traits that are somewhat resistant to such mismatch. The mismatch-resistance hypothesis provides the conceptual resources necessary for offering precisely this kind of explanation by noting that variable aspects of the environment can constitute selection pressures favoring variants that are adaptive under a broad range of environmental conditions, including some which may be entirely new to the organism. Moreover, in contrast to the Savanna Principle, which suggests that all human psychological traits are vulnerable to adaptive lag as a function of their bearers' "distance" from the EEA, the mismatch-resistance hypothesis implies that there is subset of human adaptations that are mismatch-resistant and therefore unlikely to be vulnerable to such adaptive lag, since their selected functions are to cope with complex and variable environmental conditions.

Furthermore, the concept of mismatch resistance may perhaps cast some light on the phenomenon of invasive species. Such species tend to share certain traits that increase their ecological competence and their competitive abilities in a range of different environments (Reichard and Hamilton 1997; Kolar and Lodge 2001)—traits that in other words make them relatively unsusceptible to mismatch. In fact, it seems likely that mismatch resistance and the potential for a species to become invasive will be positively related, and that there may be a number of both cognitive and noncognitive mechanisms underlying this relationship.

Evolutionary Naturalism and Human Cognition

The philosopher Alvin Plantinga has presented a pair of closely related arguments against evolutionary naturalism, which is the conjunction of the propositions that "human cognitive faculties arose by way of the mechanisms to which contemporary evolutionary thought directs our attention" (*E*), and that the God of traditional theism does not exist (*N*) (Plantinga 1993, p. 220). The proposition N is often presented as having more substantive content, but it is true that it typically involves or implies the claim that supernatural entities, like God, don't exist. The first of Plantinga's arguments attempts to demonstrate that *E&N* likely is false, given that "our cognitive faculties are reliable [...] in the sense that they produce mostly true beliefs in the sorts of environments that are normal for them" (*R*) (Plantinga 1993, p. 220).[4]

By relying on Bayes's theorem, the conditional probability of *E&N* given *R* can be calculated as follows:

$$\Pr\,(E\&N \mid R) = \frac{\Pr\,(R|E\&N\,)\cdot \Pr(E\&N)}{\Pr(R)}$$

The conditional probability of *E&N* on *R* is a function of three other probabilities, which Plantinga attempts to assign values as follows. He does not specify any value for the prior probability $\Pr(E\&N)$ but claims that it is similar to that of theism (*T*); $\Pr(R)$, he says, is close to 1; and $\Pr(R|E\&N\,)$ is low. Plantinga then rightly notes that if these assignments are correct, then $\Pr(E\&N|R)$ must be low (regardless of what $\Pr(E\&N)$ is), which means that *R* functions as an epistemic defeater for evolutionary naturalism.[5]

Plantinga's first argument has generated a lot of discussion and interest (Beilby 2002), as it suggests that the nature of human cognition may undermine any attempt at offering an adequate evolutionary explanation of its various mechanisms in purely naturalist terms. In effect, it attempts to resuscitate the conflict between Darwin and Wallace as to the origin and place in nature of the human mind. Darwin (1871) thought that the human brain and mind, including their most peculiar aspects, such as language, had evolved by natural and sexual selection, and that their various mechanisms were fundamentally continuous with those of other animal species. Wallace, however, did not believe that selection could explain human morality and intelligence, arguing instead that they were created by an intelligent designer:

> But let us not shut our eyes to the evidence that an Overruling Intelligence has watched over the action of those laws so directing variations and so determining

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[4] Although the notion of "cognitive faculties" is somewhat dated and can usefully be replaced with that of "cognitive mechanisms", this section will nevertheless for expository purposes use the same terminology as Plantinga.

[5] Plantinga is not the first to reflect on whether our cognitive faculties are reliable given their evolutionary origins, and on what a negative answer to that question would philosophically imply. Darwin (1887, pp. 315–315) expressed some worries along such lines in a letter to William Graham, and Churchland (1987) has offered some similar reflections more recently.

> the accumulation, as finally to produce an organization sufficiently perfect to admit of, and even to aid in, the indefinite advancement of our mental and moral nature. (Wallace 1869, p. 205; cf. Williams 1989, pp. 195–197)

Earlier work by Fitelson and Sober (1998) has shown that Plantinga's argument suffers from a number of problems and that it ultimately is unsuccessful. The purpose of this section is not to offer any new criticism of the argument, but rather to show how the concept of evolutionary mismatch resistance strengthens and adds to some of the criticisms already presented in the literature. For Plantinga's argument to go through, it is necessary that $\Pr(R|E\&N)$ be low; if he wants to establish the (likely) truth of theism, it should be lower than $\Pr(R|T)$. So how probable is it that our cognitive faculties produce mostly true beliefs, if evolutionary naturalism is correct? The first thing to note is that our cognitive faculties are truth-conducive with respect to some subject matters, they are unreliable with respect to other subject matters, and there are plausibly certain issues about which the reliability of our cognitive faculties is uncertain. For this reason, Fitelson and Sober (1998) note that R should be decomposed into a conjunction $R_1\&R_2\&\ldots\&R_n$, specifying the reliability of our cognitive faculties with respect to different subject matters—an idea that Plantinga appears to endorse (1993, pp. 231–232). However, having decomposed the proposition R in this manner, it is no longer clear that the conditional probability $\Pr(R1\&R2\&\ldots\&Rn|E\&N)$ is low and, in fact, it appears that it should have a higher value than the alternative $\Pr(R1\&R2\&\ldots\&Rn|T)$.

Plantinga suggests that the conditional probability of R given T should be high, since theism suggests that we have been created as "knowers" in the image of God. However, this conflicts with empirical findings that humans are subject to many decision-making biases that dispose us towards false and irrational judgments and behaviors (Bojke et al. 2021). Humans are not simply knowers and rational decision-makers, we are also often ignorant and knowledge-resistant, and our behaviors are based on flawed patterns of reasoning. Moreover, evolutionary theory can provide a good explanation for why the rationality of our beliefs and actions varies from one domain to the next (Haselton and Nettle 2006; Haselton et al. 2015). If certain kinds of rational decision require computational resources that could not have been selected for in the EEA, then we should not expect them to have been favored by evolution.

Nevertheless, it is true that humans are remarkably cognitively sophisticated, with a lot of knowledge that initially may seem puzzling from an evolutionary perspective. There are, however, two reasons why such phenomena are better explained by $E\&N$ than T. First, we know that some heuristics that appear biased actually are *ecologically rational,* in the sense that they are adapted to certain structures of the environment, for example by facilitating rapid decisions when only very little relevant information is available (Gigerenzer 1996; Gigerenzer and Gaissmaier 2011; Todd et al. 2015). By focusing on the ecological context in which the decision-making happens, and on the context in which the underlying heuristics evolved, evolutionary naturalism can explain why such ecologically rational judgments would be adaptive. Second, when it comes to the issue of how it is that we can reason and acquire knowledge about subject matters that were completely alien to our ancestors in the EEA, the mismatch-resistance hypothesis suggests that environmental complexity and variability should select for cognitive and noncognitive phenotypes that are adaptive under a range of different environmental conditions. And since such variability-selected cognitive adaptations are likely to function in a relatively domain-general manner, it follows that human should, when relying on more effortful and explicit processing, be able to acquire knowledge about a range of ancestrally foreign subject matters.

Plantinga's (1993, pp. 234–235) second argument suggests that evolutionary naturalism is self-defeating. He argues that for the person who believes the conjunction $E\&N$, R functions as a defeater for any belief that the person has, including $E\&N$, since the conditional probability $\Pr(R|E\&N)$ is low, and the (likely) truth of R is necessary for the rational acceptance of any belief. In other words, since the evolutionary naturalist is forced to accept that it is unlikely that our cognitive faculties by and large are truth-conducive, and having truth-conducive cognitive faculties is necessary for rational belief formation, evolutionary naturalism becomes a self-defeating position.

This second argument also has a number of problems that make it unsound (Fitelson and Sober 1998). Once R is properly decomposed, it is no longer clear that its conditional probability on $E\&N$ is low. Also, even if that conditional probability were low, R could still be probable given one's total evidence. There might be other reasons for thinking that our cognitive faculties are truth-conducive. Moreover, if we follow Plantinga in assuming that the *only other* reason for believing in R is T, then it is still true that evolutionary naturalism appears to provide a better explanation of why the performances of our cognitive faculties clearly vary depending on the subject matter, and of why we often reason in a manner that would have been adaptive in the EEA but not in current environments. Plantinga agrees that evolutionary naturalism occasionally might offer a good explanation of human cognitive faculties that produce true beliefs that confer a clear adaptive advantage upon the individual, but not when it comes to faculties that produce true beliefs about subject matters foreign to our evolutionary ancestors, such as science:

> So even if you think Darwinian selection would make it probable that certain belief-producing mechanisms—those involved in the production beliefs relevant to survival—are reliable, that would not hold for the mechanisms involved in the production of the theoretical claims of science, such beliefs, for example as *E*, the evolutionary story itself. (Plantinga 1993, p. 233)

Now, coming up with true theories about the universe and humankind's place in it is certainly more difficult than forming true beliefs about whether some fruit might be harmful on the basis of its sour taste and rancid smell. However, given that some of our cognitive traits are mismatch resistant, and that they function to deal with information from relatively broad content domains, it is possible to make sense of how it is that we can acquire scientific knowledge of the world in evolutionary and naturalist terms. Production of scientific knowledge might be a slow process that requires a lot of effortful and explicit processing on the part of multiple individuals that collectively work towards common goals, but it does not follow that evolutionary naturalism cannot make sense of our cognitive traits or of their (sometimes) wonderful outputs. In fact, to the extent that scientific knowledge is a product of mismatch-resistant cognitive adaptations, evolutionary theory clearly does illuminate this otherwise mysterious phenomenon.

Conclusion

That many traits retain their adaptive value in novel environments is something that needs explaining. This article has argued that the concept of mismatch resistance explains adaptation in novel environments in the same manner as the concept of evolutionary mismatch explains how traits can go from being adaptive to being maladaptive as the environment changes. Mismatch-resistant traits are expected to be favored under conditions in which complex and variable features of the environment constitute selection pressures influencing biological populations. Since variability selection has played an important role in the evolution of the hominin line—with all major events occurring under highly variable climatic and geological conditions in East Africa—there is reason to believe that some phenotypic adaptations among humans are mismatch-resistant.

The mismatch-resistance hypothesis has the potential to make progress on different issues related to evolutionary theory. Concerning the structure of the human mind, it suggests that our minds are not massively modular, in the sense that they only (or primarily) contain domain-specific mechanisms, but rather that an important subset of our cognitive mechanisms are domain general, by taking as inputs and operating on information from relatively broad content domains. In contrast to the Savanna Principle, the mismatch-resistance hypothesis can explain why it is that humans have certain evolved traits that enable them to adaptively thrive in novel environmental conditions that are radically discontinuous from those of the African savanna. And lastly, by offering an evolutionary explanation of our domain-general cognitive mechanisms and their more peculiar outputs, it helps save the naturalist philosophical framework to which evolutionary theory belongs from recent criticisms.

Funding Open access funding provided by University of Agder. The authors have not disclosed any funding.

Data availability Data sharing is not applicable to this article as no new data were created or analyzed in this study.

Declarations

Competing Interests The author has no conflict of interest to declare.

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