Invariant world, invariant mind. Evolutionary psychology and its critics

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Given the character of the evolutionary process, it is extremely unlikely that all human beings are essentially the same, but even if we are, I fail to see why it matters. Philosopher David Hull (1986, p. 4)

Progress in physics depends on the ability to separate the analysis of a physical phenomenon into two parts. First, there are the initial conditions that are arbitrary, complicated, and unpredictable. Then there are the laws of nature that summarize the regularities that are independent of the initial conditions. The laws are often difficult to discover, since they can be hidden by the irregular initial conditions or by the influence of uncontrollable factors such as gravity friction or thermal fluctuations. Physicist David Gross (1996, p. 14256)

1 Introduction

At every spatial and temporal scale, the universe varies. It is astonishing, then, that this variation can be explained in terms of (1) a small number of invariants, specifically, a few elementary particles that interact via a few fundamental forces subject to the laws of physics, and (2) the variable initial *state* of these particles, e.g., their positions and momenta.

Like physics, most scientific disciplines seek to partition the systems they study into an invariant, or nearly invariant, part, and a variable part. In chemistry, for example, a relatively few invariant elements combine to form countless distinct molecules, and in biology, an invariant genetic code with but four symbols is the basis for countless genetic sequences.

Evolutionary psychology (EP) has made a bold claim: the human brain comprises a large set of complex psychological mechanisms whose designs are invariant (i.e., universal in the species). These designs evolved by natural selection in response to a limited set of invariant properties of ancestral environments that were relevant to human reproduction, which EP dubs the environment of evolutionary adaptedness (EEA). The designs are grounded in the invariant DNA all humans share. Individuals, as I will explain here, are unique *states* of invariant complex designs, plus a small dollop of genetic noise (e.g., Tooby and Cosmides, 1990a; Hagen and Hammerstein, 2005).

Object recognition is an example of a psychological mechanism with an invariant complex design. Object recognition is computationally difficult: each particular object can produce infinitely many different images on the retina due to changes in position, angle, distance, lighting, and the presence of visual clutter (e.g., background, other objects); though we see an object many times, we never see the exact same image of it twice. Yet within 300 ms, virtually all humans effortlessly identify and categorize an object from tens of thousands of possibilities, a feat (as of 2014) beyond the capabilities of any computer (DiCarlo et al., 2012).

According to EP, much of human cognition will be similarly complex and universal, a proposition that is the brain-specific version of the more general, and much more widely accepted, claim that the human organism comprises a large set of complex evolved mechanisms, such as the heart, lungs, and kidneys, that are invariant in the species.

The claim of invariant design is restricted to *complex* mechanisms (physiological or psychological), i.e., those whose development involves the coordinated interactions of many loci across the genome (Tooby and Cosmides, 1990a). Whereas simple evolved mechanisms that are based on one or a few genes, such as skin color, often vary among populations, complex mechanisms generally do not.

Bold claims rightly attract critical attention. Some of it has come from biologists, like Stephen J. Gould and Richard Lewontin, and from behavioral ecologists, like Foley (1995) and Laland and Brown (2011). Much of it, though, has come from philosophers of science, many of whom have concluded that EP is a "deeply flawed enterprise" (Downes, 2014).

I tackle criticisms of invariant evolved psychological design in the first part of this chapter. These focus on the role and importance of "design", "function", "adaptation" and "polymorphism" in the study of life. I tackle criticisms of the EEA concept in the second part of this chapter. My responses highlight a perspective that is commonplace in EP, and among adaptationists more generally, yet which these critiques rarely acknowledge.

2 Design

The universe is a machine. Organisms are machines. Brains are machines. If, by 'machine,' we mean a system whose properties and dynamics conform to the laws of physics and chemistry, which I will refer to as the *mechanical* view, then each statement is accepted by virtually all scientists today. If, instead, we mean a system that exhibits 'design' or 'purpose,' which I will refer to as the *teleological* view, then each statement has had passionate adherents and detractors from the dawn of Western thought right up to the present. Until the Enlightenment, for instance, it was widely believed that the clock-like movement of the planets was evidence of design or purpose in nature, which then implied the existence of a Designer (God) (Ariew, 2002).

Teleological accounts of the nonliving world were defeated by the accumulating ability to explain the nonliving world in purely mechanistic terms. Examples include that the orbits of the planets are explained by the law of gravitation, that physical objects comprise atoms, and that the properties of light, electricity and magnetism are explained by Maxwell's equations. None of these explanations implies function or purpose.

The idea that, in contrast to the cosmos and all other non-living systems, organisms and their parts *are* designed or purposive, which I will term *biological teleology*, has had a very different fate. The parts of animals, such as hearts, lungs, arteries, and nerves, have been seen as serving important functions or purposes for the organism since antiquity, and this view remains the foundation of modern medicine.

The main difference between the biological teleology of Aristotle, Galen, Paley, and many others, and that of modern biology textbooks, would seem to be the explanation of the origins of design or purpose. Prior to Darwin, the intricate designs seen in organisms were, like the clockwork motion of the heavens, taken by many to be evidence of God. After Darwin, organism design was attributed to natural selection.

Much of the controversy surrounding EP involves its explicit and enthusiastic grounding in biological teleology: the brain comprises 'parts' that are 'useful,' and that usefulness explains why they are there. Human cognition exhibits all the hallmarks of design: our impressive ability to identify and recognize objects, and to construct detailed 3D models of the world from 2D stimuli; to remember vast amounts of information for decades; to learn language and countless other skills; to produce impressive tools; and to use all the foregoing to make our way in the world. These abilities are all the more impressive in light of the failure to replicate most of them in artificial systems despite well-funded efforts spanning more than half a century.

Given that the usefulness of the body's other parts, and their origin by natural selection, is relatively uncontroversial, why is EP surrounded by controversy? Many of the critics of EP are philosophers, and in philosophy, teleology has a checkered past. The philosopher Perlman (2004) explains:

> Philosophers, going back to Aristotle, used to make generous use of functions in describing objects, organisms, their interactions, and even as the basis of ethics and metaphysics. And yet, since the Enlightenment, talk of the function of natural objects, teleological function, began to be viewed with suspicion, as the mechanical model of the world replaced the old Aristotelian model. From a religious standpoint, it used to be easy to see how objects in the natural world could have natural functions, for God was said to instill functions by design throughout Creation. But philosophers became increasingly (and wisely) reluctant to invoke God to solve every difficult philosophical problem, and became unwilling to indulge in such religious explanations of teleology. It is easy to see how artifacts produced by humans would have

> functions, derived from the intentions of the human designers, but without God, it seemed impossible to believe that teleology has a place in Nature.
>
> By the twentieth century, analytic philosophers were positively allergic to any mention of teleology or teleological function.

The philosophers have a point. If organisms are physiochemical systems whose structure is completely independent of human agency, and if the properties of such systems are fully explained by physics and chemistry, then where does the 'function' or 'purpose' of their parts come from? Function and purpose seem to require intention. Without God, are these terms anything more than handy metaphors?

Functional explanations are so intrinsic to biology, however, that philosophers started taking teleology seriously again in the 1970's (Griffiths, 2011). At about the same time, a debate erupted in biology over teleological, i.e., adaptationist, explanations of behavior, especially human behavior.

The Spandrels of San Marcos (Gould and Lewontin, 1979) was perhaps the most influential contribution to this debate. Gould and Lewontin argued that the organism is like the great dome of St Mark's Cathedral in Venice, which sits atop four arches. The dome's spandrels – the triangular spaces at the intersection of two rounded arches at right angles – are, they claimed, a necessary byproduct of mounting a dome on four arches[1]. The spandrels are decorated, and

> The design is so elaborate, harmonious, and purposeful that we are tempted to view it as the starting point of any analysis, as the cause in some sense of the surrounding architecture. But this would invert the proper path of analysis. The system begins with an architectural constraint: the necessary four spandrels and their tapering triangular form.

Gould and Lewontin's charge is that students of evolution regard "natural selection as so powerful and the constraints upon it so few that direct production of adaptation through its operation becomes the primary cause of nearly all organic form, function, and behavior." Instead, they rightly argue, in organisms as in buildings, constraints and byproducts abound. According to them, the 'adaptationist programme' atomizes organisms into traits, each of which is assumed to be an adaptation; byproducts, constraints, and other alternatives to adaptation are rarely entertained. For Gould (1997a), EP committed the sins identified in the Spandrels paper:

> I shall also take up the methodology of so-called "evolutionary psychology"–a field now in vogue as a marketplace for ultra-Darwinian explanatory doctrine. Evolutionary psychology could, in my view, become a fruitful science by replacing its current penchant for narrow, and often barren, speculation with respect for the pluralistic range of available alternatives that are just as evolutionary in status, more probable in actual occurrence, and not limited to the blinkered view that evolutionary explanations must identify adaptations produced by natural selection.

The Spandrels paper had a substantial impact on philosophers of biology, who have attempted to sort out what adaptationism is, and what role it plays in evolutionary biology, which after all, also studies genetic drift and constraints. The philosopher Godfrey-Smith (1999, p. 186) identifies three possible types of adaptationism:

> *Empirical Adaptationism*: Natural selection is a powerful and ubiquitous force, and there are few constraints on the biological variation that fuels it. To a large degree, it is possible to predict and explain the outcome of evolutionary processes by attending only to the role played by selection. No other evolutionary factor has this degree of causal importance.
>
> *Explanatory Adaptationism*: The apparent design of organisms, and the relations of adaptedness between organisms and their environments, are the big questions, the amazing facts in biology. Explaining these phenomena is the core intellectual mission of evolutionary theory. Natural selection is the key to solving these problems – selection is the big answer. Because it answers the biggest questions, selection has unique explanatory importance among evolutionary factors.

> *Methodological Adaptationism*: The best way for scientists to approach biological systems is to look for features of adaptation and good design.

Empirical adaptationism is close to Gould and Lewontin's view of adaptationism, and probably that of many scholars outside evolutionary biology, and even some within it (e.g., Orzack and Sober, 1994).

Godfrey-Smith offered this typology, however, to draw attention to explanatory adaptationism, which he identifies with Dawkins. Selection might explain only 1% of all molecular genetic change, but, Dawkins and many other adaptationists would say, that is the 1% that counts (Godfrey-Smith, 2001). According to Downes (2014), EP adopts the explanatory type of adaptationism. I largely agree (but see Tooby and Cosmides, 1997, for an appeal to methodological adaptationism).

What, then, is the *scientific* status of explanatory adaptationism? Just because Dawkins and EP find these questions to be the most important, Godfrey-Smith argues, it doesn't follow that all biologists should. Explanatory adaptationism might just reflect these scientists' personal preferences. Buller (2005, p. 472) agrees:

> ...Evolutionary Psychology is adaptationist in the sense that it conceives of adaptations as occupying a more central place in our psychologies than any other psychological traits – indeed, so central a place that only psychological adaptations constitute our nature.
>
> Privileging adaptations in this way, however, and viewing them as "natural" in a way that other traits are not, has no foundation in evolutionary theory proper.

According to Godfrey-Smith, one way to defend explanatory adaptation is to appeal to what natural selection does not just for biology, but for science as a whole. By destroying the Argument from Design, natural selection is an essential pin holding together the scientific/enlightenment world view. But that means "The roots of explanatory adaptationist thinking are found not so much in biological data, but in [philosophical] views about the place of biology within science and culture as a whole" (Godfrey-Smith, 2001, p. 15). If so:

> [A]nother possible reply to explanatory adaptationism rejects the idea that the traditional problem of apparent design is a well-posed and well-motivated question, in the light of current knowledge. Rather than being a problem that has turned out to be visible and challenging from both theological and naturalistic points of view, the "problem" of design and adaptedness is itself a product of a theological view of the world. So on this view, explanatory adaptationism wrongly accepts the terms of debate favored by theological views of the world; it is the *tradition of natural theology continued* (Godfrey-Smith, 1999, p. 190; emphasis in the original).

Buller (2005, p. 475) concurs (emphases in the original):

> The problem of complex design was actually *Paley's problem.* It was the problem that nineteenth-century theologians used to challenge naturalistic accounts of the origins and complexity of life, and they chose that problem because they thought it to be unsolvable by naturalistic theories. There is nothing *in the nature of things* that dictates that the problem of complex design is central to understanding life on earth.

Downes (2014) likewise agrees that EP's adaptationism does little more than distinguish it from natural theology, creationism, and intelligent design.

2.1 Explaining explanatory adaptationism

Organisms are physical systems that must conform to physical laws, in particular, to the laws of thermodynamics. Yet the laws of thermodynamics almost seem to rule out the existence of organisms. As Erwin Schrödinger (1944), one of the architects of quantum mechanics, explained in his classic book *What is Life?*:

> When a system that is not alive is isolated or placed in a uniform environment, all motion usually comes to a standstill very soon as a result of various kinds of friction; differences of electric or chemical potential are equalized, substances which tend to form a chemical compound do so, temperature becomes uniform by heat conduction. After that the whole system fades away into a dead, inert lump of matter. A permanent state is reached, in which no observable events occur. The physicist calls this the state of thermodynamical equilibrium, or of 'maximum entropy'. ... It is by avoiding the rapid decay into the inert state of 'equilibrium' that an organism appears so enigmatic; so much so, that from the earliest times of human thought some special non-physical or supernatural force (*vis viva*, entelechy) was claimed to be operative in the organism, and in some quarters is still claimed.

Schrödinger's physicist expects a highly structured organism to quickly decay into a inert lump of matter because the vast majority of states of the organism that are consistent with its energy and composition, and are thus physically possible states, do not preserve the macroscopic structure upon which the life of the organism depends. Hence, it would seem that there is a high probability that the system of particles that is the organism would enter states in which organism functionality is degraded. Some particles of the heart could diffuse into the lungs, for instance, and vice versa, with the effect that neither the heart nor the lungs would continue to perform their functions.[2]

The perspective that is missing in many criticisms of adaptationism and EP is that a functioning organism, and its persistence for even a short amount of time, appears to be a highly improbable state of affairs (e.g., Schrödinger, 1944; Tooby et al., 2003). Gould and Lewontin's Spandrels paper, and the many criticisms it inspired, have things backward. The question is not, do noise and constraints play an important role in organism structure? The question is, why don't noise and constraints *dominate* organism structure?

Even in a well-functioning organism, such as a healthy 5-year-old girl, a tiny perturbation can quickly result in Schrödinger's "dead, inert lump of matter." Only 0.00000002 grams of botulinum toxin, produced by a food-borne bacterium (Gill, 1982), is enough to divert the 20,000 gram physical system that is the girl from a trajectory that would result in her reproduction, to a second, dramatically different outcome: death.

Over the course of human evolution the latter outcome was not the exception. For most species, including humans, most individuals die before reproducing. In human populations without access to modern birth control, a women would typically have about five-to-six live births, yet over the long term the average number that survive to reproduce can only be about two (the replacement rate), the famous observation of Malthus that so inspired Darwin. Prior to the modern era, a large fraction of all humans that ever lived died in childhood. Even today, about 5-6% of all children under 5 die, and in the 48 least-developed countries $\sim$ 13% of children die before the age of 15 (United Nations, 2011).

It is the special mechanisms – adaptations – that provide any hope of survival from one moment to the next. Interestingly, Paley (in a sermon arguing that God designed life as a state of probation, not misery) expressed a similar thought:

> In our own bodies only reflect how many thousand things must go right for us to be an hour at ease. Yet at all times multitudes are so; and are so without being sensible how great a thing it is. Too much or too little of sensibility, or of action, in any one of the almost numberless organs, or of any part of the numberless organs, by which life is sustained, may be productive of extreme anguish or of lasting infirmity. A particle, smaller than an atom in a sunbeam, may, in a wrong place, be the occasion of the loss of limbs, of senses, or of life. Yet under all this continual jeopardy, this momentary liability to danger and disorder, we are preserved. It is not possible, therefore, that this state could be designed as a state of misery, because the great tendency of the designs which we see in the universe, is to counteract, to prevent, to guard against it. (Paley and Paley, 1825, p. 43)

Drift and constraints only come into play if organisms survive and reproduce, and it is exactly this problem – survival and reproduction in a particular physical, biological, and social environment – that adaptationists are trying to solve.

The focus of Dawkins, EP, and other adaptationists on adaptation and natural selection, then, is not explained by mere personal preference nor by the role of natural selection plays in supporting a scientific worldview. Instead, it is explained by the fact that it is precisely an organism's adaptations that enable, or permit, its reproduction despite all the physical processes that militate against it.[3]

Is explanatory adaptationism, so understood, "the tradition of natural theology continued"? Natural theology also emphasized cosmological teleology: Copernicus, Kepler, Newton, and many other founders of modern science viewed their work on, e.g., the clocklike motion of the heavens, as providing evidence of a transcendent designer (Brooke, 2002). As Gillispie (1951, p. 6) argued,

> Natural philosophy and religion were not the same realm, of course, but science and theology paralleled each other in being concerned with manifestations of divinity in a universe which was assumed to be permanently divine, increasingly intelligible, and so designed that man could better his lot by improving his understanding of physical phenomena.

If adaptationism and EP are the tradition of natural theology continued, then so, too, is much of science.

Still, it is worth considering how scholars working in the tradition of natural theology could discover numerous anatomical and physiological truths. Here, the towering figure is not Paley, the eighteenth century British theologian, but Galen, the second century Roman physician and philosopher whose teachings dominated Western medicine for 1500 years. Galen was the consummate empiricist, basing his views on countless dissections and experiments. He showed that cutting the recurrent laryngeal nerves in the pig resulted in the loss of vocalization, for example, which might have been the first experimental evidence that the brain controls behavior (Gross, 1998). Such was the quality of his work that much of it is either textbook material to this day, or was the foundation for the later advances of Vesalius, Harvey, and their scientific heirs (Pasipoularides, 2014).

Galen viewed the structure of the body as the result of, and evidence for, intelligent design by a Platonic Demiurge. Unlike the Stoics, however, who argued that each kind of organism serves a purpose external to it that is established by God – the purpose of grass is to be eaten by sheep, just as that of sheep is to be eaten by man – Galen espoused an internal teleology: the parts of organisms serve the survival and reproduction of the organism itself and not some purpose external to the organism (Schiefsky, 2007). The distinction is critical:

> While the functions of the parts of an externally teleological system depend on the purpose for which the system has been designed, the functions of the parts of an internally teleological system can be understood independently of the intentions of its designer – if there is one. The parts have functions, understood as contributions to the system's continued existence, whether or not the system was designed by an intelligent agent. (Schiefsky, 2007, pp. 396-397)

Galen's empiricism and his adherence to internal teleology – a notion very similar to the views of modern anatomy and physiology and to the view that emerges from Darwinian theory – enabled him to correctly infer much about the functional structure of the body.[4]

2.2 The invariance of complex design

EP is a theory of human nature. Philosopher David Hull famously asserted that there is no such thing, specifically, that there is no set of characteristics possessed by all, and only, humans (Hull, 1978; see also Ghiselin, 1997). All humans have hearts, for instance, but so do many other animals. No nonhuman animal has language, but some people also have failed to develop language abilities, yet are still human. For Hull,

> [P]articular organisms belong in a particular species because they are part of that genealogical nexus, not because they possess any essential traits. No species has an essence in this sense. Hence there is no such thing as human nature. (Hull, 1978, p. 358)

Buller concludes his book-long critique of EP recapitulating Hull's argument (for philosophical views of human nature that are more compatible with EP, see, e.g., Machery, 2008; Samuels, 2012).

Half of Hull's argument is of little concern to EP, which does not limit itself to *uniquely* human psychological mechanisms. On the contrary, if many primate relatives had a mechanism to, e.g., learn fear of snakes, that would support the hypothesis that humans do too (and EP would count it as part of human nature).

The other half of Hull's argument, though, strikes at EP's core: many complex mechanisms are present in some humans and absent in others. Newborns cannot walk bipedally, for instance, and men lack ovaries, yet both are still human. In principle, there could even be nonsexual morphs, as there are in other species: male side-blotched lizards, for instance, have one of three different throat colors, each of which is associated with different behavioral patterns and physiology (Wilson, 1994). Hull (1986) and Buller (2005) additionally emphasize widespread genetic polymorphisms.

These apparent exceptions to invariant complex design are not really exceptions, and instead serve to clarify the concept. First, polymorphisms at loci that vary independently of one another are simple differences that EP does not expect to be necessarily invariant but that also can't explain the complex abilities of human cognition, like object recognition. Second, infants obviously possess the complex genetic design for bipedalism, but it isn't yet fully developed.

Third, most of the genes for ovaries, testes, and other important and complex sex differences reside on autosomes (or on the X-chromosome), which, across generations, spend half their time in male bodies and half in female bodies[5]. Thus, males possess the design for ovaries (which is not expressed in males), and females possess much of the design for testes (which is not expressed in females). The difference is the presence or absence of a genetic switch, the Y-chromosome[6]. Similarly, in many polymorphic species, most of the genes for all morphs seem to occur in all individuals – the design is shared, just as it is with sexual morphs. What differs is the presence or absence of a genetic or environmental switch that determines which design is expressed[7].

The reason that complex functional differences among morphs in the same species are typically based on genetic switches, rather than large suites of interacting alleles that are unique to each morph, is that the latter genetic architecture is unstable: sexual reproduction and recombination quickly erode associations among alleles at multiple loci, and even a small amount of migration quickly erodes genetic differences between populations.[8]

Thus, EP and other evolutionary biologists locate invariant design in the DNA-encoded developmental programs that generate complex phenotypes during ontogeny (e.g., Tooby and Cosmides, 1990a; Hagen and Hammerstein, 2005).

2.3 The individual is a unique realization of invariant design

Though the design of a complex psychological mechanism – its underlying developmental program – is invariant, the neurological mechanism it generates need not be. Invariant developmental programs, typically, evolved to read environmental inputs, which can alter the assembly of the mechanisms in principled ways. The language circuitry of a native Chinese speaker might differ from those of a native English speaker, for instance (e.g., Tooby and Cosmides, 1990a; Geary and Bjorklund, 2000; Hagen and Hammerstein, 2005).

Complex functional differences among individuals, then, are probably not due to differences in design (i.e., suites of interacting alleles that are present in some individuals but not others), but to age- and sex-specific differences in the expression of a shared design during development, differences in expression due to differences in the condition of the environment or organism, differences in genetic and epigenetic switches (e.g., Haig, 2007), or perturbations due to mutations or disrupted development.

Even when there are no functional differences between individuals, invariant designs will still give rise to enormous inter-individual variation because evolved mechanisms typically have multiple states. The *raison d'être* of psychological mechanisms is to read and respond to environmental input. Because no two individuals inhabit identical environments or have identical sequences of experiences, and because each individual has a unique dollop of genetic noise, the joint *state* of an individual's psychological mechanisms is unique. Each individual has been exposed to an overlapping but not identical set of objects during his or her life, for example, and thus has a unique ability to recognize a particular large set of objects. The states of invariant memory mechanisms, emotion mechanisms, hunger mechanisms, and so forth, are all contingent on individual experiences and circumstances. A hypothetical brain with but 30 independent invariant mechanisms, each of which had only two states, would have, altogether 2^{30}, or about 1 billion possible states. According to EP, the human brain comprises hundreds or thousands of evolved mechanisms, most of which can be in multiple states contingent on conditions during development and the current environment. It is obvious that although the designs are invariant, the joint state of the phenotype is unique for each individual (Tooby and Cosmides, 1990a; Buss, 2009).

Hagen and Hammerstein (2005) frame this perspective in strategic terms. The genome encodes a strategy that is shared by all members of the species. During development, each individual makes a different series of 'moves' that depend on environmental circumstances or the inherited values of genetic and epigenetic switches. 'Male,' 'female,' and other morphs are such 'moves,' and a phenotype is thus a state of play.

3 The EEA

For a new allele to increase to high frequency in the population, it must cause some particular effects that (on average) increase the reproduction of the organism in which it resides, and it must do so for, typically, many hundreds or thousands of generations. For the allele to persistently cause these effects, the environment with which it is interacting, which can include the organism itself, must have persistent properties. This does not mean that the target environment does not vary, but rather that variation is governed by unchanging rules or statistical patterns. The varying world, in other words, is a consequence of a deeper, invariant structure.

This invariant structure includes mathematical properties, such as the rules of arithmetic; physical and chemical laws, such as the laws of optics and conservation of energy; and 'looser' statistical regularities, such as spiders and snakes are often venomous. Invariant designs evolve to reliably manipulate the variable environment by exploiting its underlying invariant structure.

Even associative learning depends on environmental regularities: it would be pointless to learn to associate a stimulus with food today if that stimulus did not predict food tomorrow. That the world is rife with shorter-term associations is itself an invariant that underlies the evolution of associative learning mechanisms.

EP uses the term EEA in two senses: to refer to the entire set of environmental regularities that were relevant to human evolution, and, as discussed shortly, to refer to adaptation-specific regularities. It is the latter that is the basis of specific EP research programs.

EP often equates the human EEA, in its broad sense, with the Pleistocene, which began 2.6 million years ago[9] and ended about 10,000 years ago. This choice was motivated by four facts: the first members of the genus *Homo* appear in the African fossil record near the beginning of the Pleistocene; there was sufficient time during the Pleistocene for new complex adaptations to evolve; near the end of the Pleistocene modern humans had completed a global expansion out of Africa and were starting to transition to an agricultural lifestyle, which brought profound changes in, among other things, diet, disease, and settlement pattern; and new complex adaptations could not have evolved in the last 10,000 years.

I will address four common criticisms of the EEA, one of the most controversial concepts in EP.

3.1 Is the EEA unknowable?

For many purposes the study of present environments as models of past environments are our best window on the past, because an enormous number of factors, from the properties of light to chemical laws to the existence of parasites, have stably endured. Tooby and Cosmides (1990b, p. 390).

Many critics have argued that we don't know, and perhaps can't know, much about how our Pleistocene ancestors lived, so the EEA concept is, at best, uninformative, and at worst invites groundless speculation and storytelling. Gould (1997a), for example, wrote that evolutionary psychologists "have made their enterprise even more fatuous by placing their central postulate outside the primary definition of science – for claims about an EEA usually cannot be tested in principle but only subjected to speculation." Ironically, Gould was a paleontologist whose own research involved testing claims about the distant past. Buller (2005, p. 93), another critic, says "[W]e can't specify the adaptive problems faced by our ancestors precisely enough to know what kinds of psychological mechanism would have had to evolve to solve them." Laland and Brown (2011, p. 177) similarly say "What is wrong with the notion of the human EEA as a particular time and place? The problem is that comparatively little is known about the lifestyle of our ancestors throughout the Pleistocene. Consequently, the EEA concept has engendered a wealth of undisciplined speculation and story-telling in which virtually any attribute can be regarded as an adaptation to a bygone Stone-Age world." Richardson (2007, p. 41) says "Direct evidence concerning ancestral environments, variation, social structure, and other relevant features are often not available, though they sometimes are."

The criticism that we don't, or can't, know much about the human EEA is a strong claim with profound consequences for any evolutionary analysis of the human organism, including its cognitive functions. Adaptations evolved to manipulate aspects of the environment. If the environment is unknown, it would be difficult, and perhaps impossible, to make much sense of the adaptation. Because many EP critics accept that the functional properties of organisms evolved by natural selection, their claim that the human EEA is mostly unknown, and often unknowable, entails the claim that the evolved functions of the body, including the brain, will remain mostly unknown. These include all evolved cellular functions (including neural functions), the immune system, organs, bones, and the rest. This conclusion seems absurd. If it were true, the critics should worry much more about the billions of dollars spent every year on research to elucidate all these functions than they should about the relatively small group of evolutionary psychologists (Hagen, 2005).

How mysterious, then, is the human EEA? If the EEA were *completely* unknown, we would have to consider that it might have resembled any possible environment. Did humans evolve in a galactic dust cloud? Did they evolve on a gas giant, like Jupiter? Did they evolve in the asteroid belt, or on a planet like Mars or Venus? Did they evolve in the oceans of earth, or among the giant dragonfly-like insects of the Carboniferous, or during the time of the dinosaurs?

No, *Homo* evolved in the terrestrial environments of Africa and Eurasia during the last 2 million years, which, in evolutionary terms, is relatively recently. The giant insects of the Carboniferous were gone, the dinosaurs were gone. Many of the plant and animal taxa of the Pleistocene are similar to those that exist today. Physics and chemistry were the same – the refractive index of the atmosphere was close to 1, for example, just as it is today. Geology was the same. Much of the ecology was similar to what we see today. Our bodies were almost the same. Even the social environment was not so different: there were people of various ages and both sexes, that lived in groups, that were healthy and sick, that were of varying degrees of relatedness, and so on.

Some critics acknowledge that aspects of the environment in which humans evolved are known, but nevertheless argue that the selective pressures that acted on human cognition might never be understood well enough. Along these lines, Sterelny and Griffiths (1999) raise a 'grain' problem, which is taken up by Buller: "It is true that we can always be certain that just about all sexually reproducing species face the adaptive problems of selecting mates of high reproductive value and inducing potential mates to become actual mates. These descriptions of adaptive problems are so coarse-grained, however, as to be wholly uninformative about the selection pressures that act on a species" (Buller, 2005, p. 97).

To illustrate the problem, Buller notes that although all male birds must attract mates, different species do this in very different ways: the male bowerbird must build an ornate bower, for example, whereas a male sedge warbler must sing a wide repertoire of songs. Thus, although at a coarse grain males of both species face the same problem, at a finer grain the males face very different problems – building bowers vs. singing – and hence different selection pressures on their cognitive evolution. Buller concludes "[S]imply knowing that Pleistocene humans needed to attract mates doesn't inform us of the subproblems that constituted that adaptive problem for Pleistocene humans. And it is those more specific subproblems that adaptations would have evolved to solve. In order to get the more fine-grained and informative description of the subproblems, however, we would need to have more detailed knowledge of the lifestyles of our ancestors. And that's knowledge we simply don't have" (Buller, 2005, p. 98).

How, then, can Buller write confidently about the evolved strategies of male bowerbirds and sedge warblers, about whom we have even *less* direct evidence of ancestral lifestyles (e.g., Naish, 2014)? Buller is inferring the mate attraction strategies of ancestral birds from the strategies of living birds, of course, but apparently is not willing to do the same with humans.

Sterelny and Griffiths (1999) and Buller (2005) both argue, in addition, that because human cognitive evolution was driven by a social arms race (they claim), there was no stable EEA to which to adapt:

> According to [the Machiavellian] hypothesis, our mental capacities evolved in an "arms race" with human populations....If the selection pressures important in cognitive evolution derive from interactions within the group, then selective environment and adaptive response change together. There is no invariant environment to which the lineage is adapted. (Sterelny and Griffiths, 1999, p. 328)

Pitting the arms race concept against the EEA concept is puzzling (Machery and Barrett, 2006). First, arms races have produced some of the most spectacular and indisputable examples of adaptation known to science – the speed of cheetahs and gazelles, the jaw-dropping camouflage of leaf insects, the sophistication of the immune system and of the pathogens that evade it. Second, as such examples make clear, arms races often (though not always) produce strong *directional* selection: fast gazelles select for faster cheetahs, which select for faster gazelles, and so forth. In these cases, the EEA is especially well defined. Third, the social arms race idea is not a core premise of EP. Instead, it is a very specific empirical claim about the human EEA, which is why the evolutionary psychologists who have developed versions of it (e.g., Flinn et al., 2005; Miller, 2001) have invested considerable effort in providing the necessary theoretical and empirical support. Their main thesis is that a social arms race created strong directional selection on human intelligence, which would explain the evolution of exceptional human brain size and the corresponding cognitive abilities. Ultimately, it seems contradictory to ground one's argument that we can't know anything useful about the human EEA, or there was no stable EEA, in a claim that, actually, it was a social arms race.

Given that the critics from philosophy accept that adaptations evolve by natural selection, and that 'selection' entails interaction with the environment, why, exactly, are they skeptical that we can study this (past) environment? Is their acceptance of evolution by natural selection merely *pro forma*?

The philosophers worry about two types of reasoning. I already discussed the first, which Machery (2011) refers to as the 'forward-looking heuristic.' It begins by identifying an adaptive problem in the EEA (e.g., mate attraction) and then posits a solution (e.g., a mate attraction strategy). The grain and arms race problems target this type.

The second line of reasoning, often described as 'reverse engineering,' or the backward-looking heuristic (Machery, 2011), begins with some organism trait that exhibits evidence of 'design,' and then attempts to infer the adaptive problem that it evolved to solve (e.g., human males have a propensity to take unnecessary risks; this propensity would have helped signal good genes to females). Reverse engineering is also thought to have problems. For example, the Archaeopteryx foot exhibits design for grasping, but did it evolve to grasp branches (i.e., perching), which would support the hypothesis that this species was well-adapted for flight, or did it evolve to grab prey, which would support the alternative hypothesis that Archaeopteryx was a terrestrial predator (Richardson, 2007)?

Used separately, these two types of arguments each do have limitations. Used together, however, and in combination with well-tested theories from evolutionary biology, they are able to make genuine contributions to understanding human evolution. Machery (2011) points out that although EP contends that the forward-looking heuristic is useful, it does not claim that it is necessary; that EP usually posits several competing hypotheses (e.g., multiple possible mating strategies); and that EP draws on several bodies of knowledge to constrain hypotheses. In addition, the backward-looking heuristic can bootstrap the forward-looking one: the universal aspects of mate preferences of contemporary women provide a decent hypothesis for the mate preferences of ancestral women, for instance, just as those of living female bower birds do for ancestral ones. These hypothesized ancestral female preferences are then essential components of the EEA of male mating strategies of humans and bower birds, respectively. Machery concludes "Although clearly fallible, the discovery heuristics and the strategies of confirmation used by evolutionary psychologists are on a firm grounding." See also Machery and Barrett (2006); Machery and Cohen (2011).

In short, the environments of the last 2 million years were highly structured and exhibited many regularities, enough to keep EP busy for a long time.

3.2 The EEA, or EEA's?

Many critics have complained that because environments always vary, especially during the Pleistocene, there was no singular EEA. At best, there were multiple EEA's (e.g., Foley, 1995; Smith et al., 2001; Laland and Brown, 2011). These critics are often conflating the variable state of an environment with its invariant properties.

In addition, the EEA concept has a narrower sense that is "adaptation-specific" (Tooby and Cosmides, 1990b, p. 388) or "adaptation-relevant" (Tooby and Cosmides, 1990b, p. 390). These are the environmental properties that are important to one particular adaptation's development and functioning but might be irrelevant to other adaptations. Irons (1998) developed a similar concept, using the similar term "adaptively relevant environment" (ARE).

To illustrate: to focus light on the retina, the cornea and lens must have very special shapes that depend on the refractive index of air, which is about 1. The human eye would not work well if this refractive index were much different, and indeed, humans do not see well in water, which has a refractive index of 1.33. The adaptation-relevant EEA of the human cornea and lens therefore includes the refractive index of air. The EEA of the cornea and lens does not include gravity, however, because it does not play a role in the refraction of light, even though it does play an essential role in, e.g., human locomotor adaptations.

The distance of objects from the eye was also an 'adaptation-relevant' aspect of the ancestral environment. But unlike the refractive index of air, the distance of objects from the eye obviously varied constantly. There are, however, fixed laws of optics. These permitted the evolution of a mechanism that adjusts the curvature of the lens to enable focusing on objects from a few centimeters out to infinity.

Thus, in a species, there is a separate EEA for each adaptation, which for humans number in the many thousands. Moreover, because variation in adaptation-relevant properties often has underlying regularities, mechanisms can evolve to respond to it.

3.3 Evolution before the Pleistocene

Critics point out that the human EEA could not begin with the Pleistocene because many human adaptations evolved much earlier. Downes (2009, p. 250), for instance, says "Components of this account [of the evolution of the human mind] will come from various times in our evolutionary history, including the Pleistocene, but also including times long before and long after this period....[T]he contribution of [EP] to understanding human evolution is limited by an adherence to the thesis that our minds are a product of the Pleistocene Epoch. Actually, more is gained by rejecting this thesis than by retaining it." Laland and Brown (2011, p. 179) similarly remark, "Comparative analyses of animal abilities suggest that many human behavioural and psychological traits have a long history. Some human behavioural adaptations, such as maternal care or a capacity to learn, may even have evolved in our invertebrate ancestors. Many perceptual preferences will be phylogenetically ancient."

EP agrees:

> To the extent that there is an ambiguity in the concept of the environment of evolutionary adaptedness, it is because of the time-dimension of the problem. Because the history of any evolving lineage extends back several billion years to the origins of life, the characterization of ancestral conditions requires a time-structured approach matching specific statistical environmental regularities against specific instances of evolutionary modification in design" (Tooby and Cosmides, 1990b, p. 387-388).

To illustrate the "time-structured approach" with the cornea and lens: the vertebrate eye evolved in a marine environment c. 500 million years ago, in which the refractive index of water, 1.33, was an invariant, adaptation-relevant property leading the evolution of a spherical lens in fish. With the evolution of terrestrial animals, c. 400 million years ago, the refractive index of air, about 1, was now critical, leading to the evolution of a much flatter lens. Both dates differ dramatically from the EEA for other human adaptations, like the pelvis, knee, and foot, whose morphologies in hominins evolved perhaps 3-6 million years ago, enabling bipedal locomotion.

If the purpose of the analysis is to understand why modern humans retained an adaptation inherited from nonhuman ancestors, like the lens, then its EEA – and this is what almost all critics miss – is the period of most recent *stabilizing selection* on that adaptation:

> To the extent that the adaptation has assumed an equilibrium design under stabilizing selection, the period of stabilizing selection itself becomes a primary part of the EEA...." (Tooby and Cosmides, 1990b, p. 387-388).

To a close approximation, the complex design of the human organism was either stabilized by selection during the Pleistocene, in the case of the many adaptations inherited with little modification from pre-Pleistocene ancestors; or newly evolved during the Pleistocene, in the case of human-specific adaptations like language.

3.4 Recent human evolution

A persistent criticism of EP is that human evolution did not stop when the Pleistocene ended 10,000 years ago, as the EEA concept seems to imply. Foley notes "If the EEA is a uniform background to which all humans adapted in the past, then this of course greatly limits the scope for selection operating today. The EEA has the effect of fencing evolutionary processes firmly into the past" (Foley, 1995, p. 194). Buller argued "Thus, it is safe to conclude that radically changed environments since the Pleistocene have created strong selection pressures favoring psychological evolution" (Buller, 2005, p. 110). Moreover, "the nearly four hundred human generations since the end of the Pleistocene has certainly been sufficient time for selection-driven evolution in human psychological traits. Thus, it is overwhelmingly likely that there has been some adaptive psychological evolution since the end of the Pleistocene, which has rendered contemporary humans psychologically different from their Pleistocene ancestors" (Buller, 2005, pp. 111-112). Laland

and Brown (2011, p. 181) similarly question “[a]ny assumption that natural selection on humans has stopped....”

Two important factors affect the rate of adaptive evolution, and thus the likelihood of recent human cognitive evolution: environmental change and population size. If the environment has changed substantially, then new adaptive mutations can experience particularly strong selection relative to the now less well-adapted alleles already present in the population. In larger populations, there will be a greater absolute number of mutations per generation than in smaller populations (everything else equal), and hence more adaptive mutations for selection to act on. Both these factors apply to humans.

The population of *Homo sapiens* began to grow in the late Pleistocene, c. 50 kya, and this growth accelerated with the advent of agriculture at the start of the Holocene, about 10 kya. The transition to agriculture, itself probably made possible by the environmental change that marked the end of the ice age (Richerson et al., 2001), brought further changes in diet, population density, settlement pattern, and disease. Analyses of genetic variation in modern humans indeed reveal signatures of the recent acceleration of positive selection (Hawks et al., 2007; Cochran and Harpending, 2009). Humans have evolved since the end of the Pleistocene.

EP certainly acknowledges important environmental change and population growth since the end of the Pleistocene. In fact, these are cornerstones of its argument that the EEA largely corresponds to the Pleistocene. It also agrees that recent positive selection occurred, tipping its hat to the evolution of lactase persistence and malaria resistence (Tooby and Cosmides, 1990a), classic examples of adaptive evolution during the Holocene. Why, then, would it downplay the possibility of recent adaptive evolution of cognition?

3.4.1 Racism and Genocide

In 1975, E. O. Wilson published *Sociobiology: The new synthesis*, which summarized recent work on social evolution by many evolutionary biologists. Wilson also briefly noted that these theories could help explain human behavior. In response, a number of academics, including Stephen J. Gould and Richard Lewontin, wrote a letter to the New York Review of Books with the following passage (Allen et al., 1975):

> These theories provided an important basis for the enactment of sterilization laws and restrictive immigration laws by the United States between 1910 and 1930 and also for the eugenics policies which led to the establishment of gas chambers in Nazi Germany.
>
> The latest attempt to reinvigorate these tired theories comes with the alleged creation of a new discipline, sociobiology.

This was the opening shot in the sociobiology controversy of the 1970's and 1980's, much of it driven by the fear that sociobiology, applied to humans, would justify racism and eugenics. The controversy limited sociobiology – now renamed behavioral ecology – mostly to the study of nonhuman organisms. EP, while rejecting this judgment of sociobiology, did not want to suffer the same fate.

Because racists and eugenicists typically justify discrimination (and worse) by claiming that one population is biologically superior to another, EP has taken great pains to ground itself in theory and evidence of a *universal* human nature that evolved, or was maintained by stabilizing selection, during the roughly 2 million years of the Pleistocene. If EP is correct, then there are no fundamental biological differences among human populations, let alone any notion of 'biological superiority.'

Unfortunately, human migration during the late Pleistocene created conditions that were amenable to the evolution of differences among populations, potentially including cognitive differences, that could be used to justify discrimination. About 60 ka, modern humans dispersed out of Africa into somewhat geographically and genetically isolated populations in Europe, Asia, Oceania, and the Americas, each characterized by distinct environmental conditions. This population structure, combined with prolonged, exponential population growth during the last 10,000 years, was conducive to genetic divergence of populations due to selection. In humans, then, recent evolution would tend to go hand-in-hand with *population-specific* evolution.

3.4.2 Genetic variation in the human species

The human genome contains about 3 billion bases. About 1% codes for proteins and another 3% – 15% is under selection, i.e., serves functions such as gene regulation (a recent estimate is 8.2%; Rands et al., 2014).[10] Thus, most DNA is nonfunctional. The functional part of the genome is still very poorly understood; it is not even entirely clear which sequences in the genome are functional.

Across the entire genome, any two humans, on average, are identical at >998 of every 1000 bases (Barbujani and Colonna, 2010). In protein coding and other functional regions, they are identical at >999 of every 1000 bases, presumably due to purifying selection (Tennessen et al., 2012; Ward and Kellis, 2012). Human genetic variation is substantially lower than that seen in other primate species, probably due to an especially small ancestral population size (Marques-Bonet et al., 2009).

Of the bases that vary, rare variants vastly outnumber common ones. Most rare variants are recent mutations that are neutral or weakly deleterious and have not yet been eliminated by purifying selection. Because most of the genome is nonfunctional, most genetic differences between individuals are nonfunctional differences.

The low levels of genetic variation across the human genome, even lower levels in functional regions, and the concentration of this variation in rare alleles, most of which are neutral or deleterious, all support the EP view that there is a set of complex human physiological and psychological adaptations that is based on a universal genetic architecture that evolved by natural selection.

3.4.3 Recent evolution and genetic diversification

It might be the case, though, that important aspects of this universal genetic architecture evolved during the last 10,000 years. It might also be the case that the functional variation that does exist contributes to adaptive cognitive differences between populations.

Social scientists have long accepted Lewontin's argument that because there is greater genetic variation within human populations than between them,

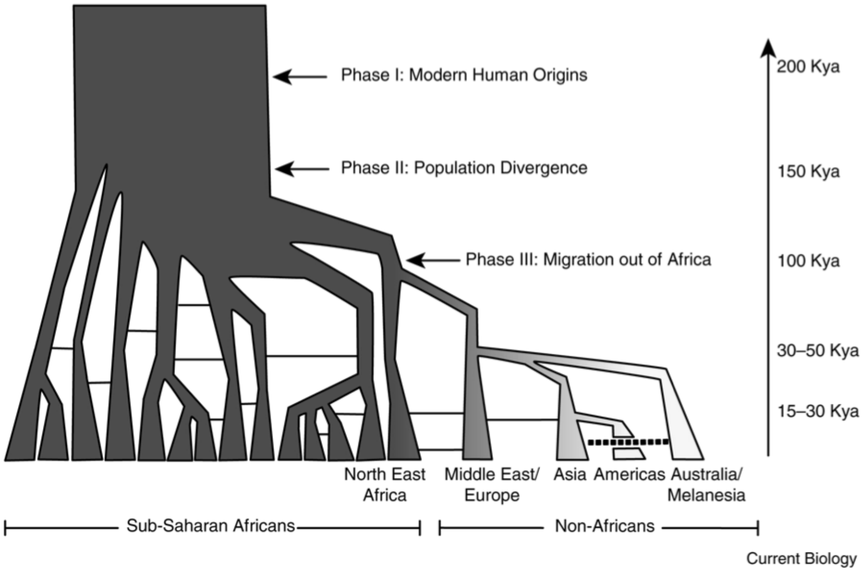

Figure 1: Decreasing intensity of color represents the concomitant loss of genetic diversity as populations migrated in an eastward direction from Africa. Solid horizontal lines indicate gene-flow between ancestral human populations and the dashed horizontal line indicates recent gene-flow between Asian and Australian/Melanesian populations. Figure and caption from Campbell and Tishkoff (2010).

genetic differences among populations are unimportant (Lewontin, 1972).[11] Alleles do not vary independently across loci, however. By taking account of the correlation of alleles across many loci, it is possible to classify individuals into groups based on ancestry (Edwards, 2003). At the same time, group boundaries are not sharp, or even entirely consistent across studies, and some variation is better explained by clines than clusters (Barbujani and Colonna, 2010).

Analyses of genetic variation in contemporary human populations, combined with archaeological evidence, support the following scenario. Modern humans evolved in Africa by c. 200 thousand years ago (kya). Between 200 and 100 kya, modern humans diverged into distinct subpopulations within Africa, albeit with admixture. The effective population size might have been about 7000-15,000. Sometime between 100 and 50 kya, one or more small groups of Africans, perhaps as few as 1000 individuals, migrated out of Africa. These migrants did not contain all the genetic diversity in the African population. Instead, they came from one or a few African subgroups. The migrant population expanded in the Middle East, interbred with local archaic human populations (e.g., Neanderthal-derived DNA accounts for an estimated 1-4% of the Eurasian genome), and subsequently migrated to Europe, Asia, Oceania, and the Americas. With each migration there was a loss of genetic diversity, probably due to a serial founder effect. At the end of the Pleistocene, every continent (except Antarctica) was populated and each non-African population exhibited a subset of the common genetic variants found in Africa (Barbujani and Colonna, 2010; Campbell and Tishkoff, 2010; Henn et al., 2012). See figure 1.

The now global human population exploded during the Holocene, almost certainly due to the transition to agriculture. This explosion generated the large number of rare variants noted earlier, most of which are of recent origin (5-10 kya) and more-or-less specific to the major continental populations. Thus, there has been recent genetic divergence among the continental populations, but much of this variation – perhaps 95% – is neutral or weakly deleterious (Fu et al., 2013; Fumagalli et al., 2011; Tennessen et al., 2012).

3.4.4 Recent positive selection

Despite the foregoing, evidence has been accumulating for over half a century that the human species has undergone at least some recent adaptive evolution. It does not appear to have acted uniformly on the human species, however, but instead has driven divergence among the major continental human groups (though results to date might reflect methodological limitations; Lachance and Tishkoff, 2013).

Although most studies of recent positive selection in humans have focused on hard sweeps – new mutations that sweep to fixation – theory and evidence suggest that most recent positive selection has instead been on standing variation – alleles that were common prior to the onset of the new selection pressure, or simultaneous selection on multiple loci (Hernandez et al., 2011; Tennessen and Akey, 2011).

Regions of the genome that have apparently experienced recent positive selection often contain multiple genes and numerous nucleotide polymorphisms, hampering identification of the target of selection, but studies have consistently fingered climate, subsistence, sexual selection, and especially pathogens as probable selection pressures (Fumagalli et al., 2011; Fu and Akey, 2013; Lachance and Tishkoff, 2013). In only a very few cases, however, such as adaptation to high altitude, lactase persistence, and malaria resistance, have the selected variant, phenotype, and selection pressure all been pinpointed.

Regarding recent cognitive evolution, Huang et al. (2013) conducted a meta-analysis of 27 studies of positive selection across the human genome and found that genes that are highly expressed in the central nervous system are enriched in recent positive selection. Keeping in mind that false positives are common in studies of positive selection, possible examples of divergent positive selection on neural function include: opioid cis-regulatory alleles (Rockman et al., 2005); loci involved in the axon guidance pathway, which determines the direction the axon will grow, ultimately influencing the development of neuronal networks (Tennessen and Akey, 2011); genes in non-African populations in the neuregulin ERBB4 signaling pathway, which is involved in the development of the nervous system, heart, and other tissues (Pickrell et al., 2009); selection of downstream gene targets of FOXP2, which is implicated in language abilities, in a European sample but not an

East Asian or African sample (but the selected downstream genes have multiple functions in neural and non-neural tissue) (Ayub et al., 2013); and alleles in Ashkenazi Jews that have been argued to increase intelligence in heterzygotes but cause severe disease in homozygotes (Cochran and Harpending, 2009).

In none of these examples are the phenotype and selection pressure well understood. It is quite possible that selection was on non-neural aspects of the phenotype (i.e., pleiotropy). It is also possible that, due to convergent evolution, population divergence in genes underlying neural pathways resulted in little divergence in neural/psychological function. Additionally, population differences in frequencies of alleles impacting neural function might be due to founder effects and drift. Such seems to be the case with the dopamine D4 alleles (Kidd et al., 2013).[12] Finally, because exposure to neurotoxins from plants, fungi, pathogens, and the environment varied across populations, some divergent neural evolution might represent protective changes in neuroreceptors and other neural functions.

Nevertheless, despite the lack of compelling evidence to date, it would not be surprising if there were limited population divergence in some neural/psychological functions due to recent positive selection on cognition and behavior.

3.4.5 Recent positive selection and complex design

Given the possibility of divergence in neural function, it would be unsatisfying, to say the least, if EP's claim of a universal evolved human psychological design were grounded in moral and political concerns about racism, and had little basis in science. It is reassuring, then, that more than 2000 years of research in anatomy and physiology, more than a century of research in cellular biology, and more than half a century of research in molecular biology – including all their neuro-specific versions, such as neuroanatomy, neurophysiology, and neurobiology – has found profound similarities in evolved function within the human species, and even across species. The complex design that defines the human organism is, to a close approximation, universal in the species.

Known, recently evolved population differences in physiology are limited to relatively simple modifications of this universal design, often involving changes to only a single nucleotide. The sickle cell trait, for example, which protects some populations from malaria, is a point mutation in the hemoglobin gene (the protective mechanism is still uncertain). Lactase persistence in some populations is due to a point mutation in a regulatory region of the lactase enzyme. Population differences in skin color are primarily due to differences in melanin pigment production by cutaneous melanocytes (the genetic mechanisms are still not well-understood).

The reason there are no complex adaptive differences between the continental human populations, despite their relative genetic isolation (but see Hellenthal et al., 2014), is simply that there hasn't been enough time for them to evolve. Physicist Greg Cochran and population geneticist Henry Harpending, who argue for the importance of recent adaptive divergence in human populations (Cochran and Harpending, 2009; Hawks et al., 2007), concede this point:

> ...John Tooby and Leda Cosmides (two of the founders of modern evolutionary psychology) have said that "given the long human generation time, and the fact that agriculture represents less than 1 percent of the evolutionary history of the genus *Homo*, it is unlikely that we have evolved any complex adaptations to an agricultural (or industrial) way of life." A complex adaptation is a characteristic contributing to reproductive fitness that involves coordinated actions of many genes. This means that humans could not have evolved wings, a third eye, or any new and truly complicated adaptive behavior in that time frame. Tooby and Cosmides have argued elsewhere that, therefore, deep mental differences between human populations cannot exist.
>
> We think that this argument concerning the evolution of new complex adaptations is correct, but it underestimates the importance of simple adaptations, those that involve changes in one or a few genes. (Cochran and Harpending, 2009, p. 9-10)

For Cochran and Harpending, "importance" does not mean profound changes in design but rather profound effects on human history and prehistory, such as the spread of the Proto-Indo-Europeans (which they attribute to the evolution of lactase persistence).

In summary, the genetic evidence is consistent with the view that the evolved designs of humans' psychological mechanisms are either (1) universal, (2) slightly modified versions of universal designs, or (3) new, very simple, and population specific.

4 Concluding remarks

Most EP critics accept most of the major tenets of EP: the blank slate is untenable, functions evolve by natural selection, and an evolutionary perspective will consequently be important to understanding human brain function. Most critics also understand that EP is science, and that it will ultimately stand or fall on the empirical evidence. In a review of *Alas, Poor Darwin: Arguments against Evolutionary Psychology*, philosopher David Hull, himself a critic of EP, concludes

> Rose and Rose remark that "bad theory can never be driven out solely by criticism". If so, the critics of evolutionary psychology could make better use of their time by developing these alternative theories, no matter how complicated they turn out to be. Repeating overly familiar criticisms of evolutionary psychology and sociobiology is unlikely to have much effect. For all their crudity and lack of sophistication, evolutionary psychologists keep churning out book after book, paper after paper, both popular and technical. They are not content to carp on the sidelines. (Hull, 2000, p. 125)

As this Handbook testifies, indeed we are not.

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Notes

[1] There have been many criticisms of the Spandrels paper, including that the architectural feature is actually called a *pendentive*, that pendentives play an important structural role in supporting both the arches and the dome, and that this design was chosen over others because it was better suited for displaying Christian iconography, the *raison d'être* of St Mark's. Hence, the spandrels of San Marcos *are* functional and the term 'spandrel' is therefore a poor choice to refer to byproducts of adaptations. See, e.g., Dennett (1995); Mark (1996); Houston (2009); cf. Gould (1997b).

[2] It is well-known that organisms do not violate thermodynamic law because they are not isolated systems: by drawing on an external source of what Schrödinger (1944) refers to as negative entropy (e.g., the sun), it is possible for a highly ordered system, like an organism, to maintain its order by increasing the disorder of the external environment. What is less widely recognized, however, is that no one knows exactly how this happens. The physics of systems at (or close to) thermodynamic equilibrium is well understood. There is no complete and unified theory of systems that are far from equilibrium, however, which includes life. As Qian (2007) remarks, "How is it possible to develop mathematical models of cellular processes such as gene regulation and signal transduction if even the underlying basic physical chemistry is still not in hand?"

Stotz and Griffiths (2003), on the other hand, criticize EP for, among other things, "redefining negentropy itself as functional design (!)...." But EP has done no such thing. EP, along with most evolutionary biologists, has merely claimed that *functional* organization would not arise without natural selection. That many nonliving systems exhibit order (but not functional order!) is commonplace and not disputed by EP. On the contrary, order in the nonliving world is essential to the EEA concept, discussed in section 3.

[3] Some adaptations are strictly necessary for reproduction, others simply increase the probability of reproduction.

[4] While there is clear overlap between the functions of Galen and the adaptations of evolutionary biology, there are also substantial differences. For instance, Galen, like Aristotle, thought that some organs existed not simply to make life possible but to make life better – to serve well-being or the 'best life' (Schiefsky, 2007). Adaptations have no such function. Conversely, adaptations can have properties that, for Galen and Paley, might have been inadmissible, such as trading off survival for reproduction.

[5] The X-chromosome spends 1/3 of its evolutionary history in males

[6] The Y-chromosome is small, and because a single gene on it, SRY, initiates male sexual differentiation, it can be thought of as a genetic 'switch' that activates one of two genetic designs, both of which are present in both sexes. Recently, though, other male-specific genes have been discovered on the Y-chromosome. This male-specific region seems to mostly involve genes that are expressed in the testes (e.g., Hughes et al., 2010).

[7] By genetic switch I mean a single locus, or a very small number of loci, that regulates expression of many loci; alleles at the switch locus then 'toggle' development of different complex morphs.

[8] There are genetic mechanisms other than switches that might underly complex polymorphism in some species, and if these occurred in humans they might constitute genuine exceptions to EP's claim of an invariant complex evolved design. For review, see Mckinnon and Pierotti (2010).

[9] Until recently, the beginning of the Pleistocene was placed at 1.8 million years ago. However, there has long been a consensus that it should be placed at the first evidence

of climatic cooling of ice-age magnitude, which is now known to have occurred earlier, c. 2.6 million years ago, perhaps triggered by the closing of the Panama isthmus (Cohen and Gibbard, 2010).

[10] A large consortium claimed to have assigned biological functions for 80% of the genome (The ENCODE Project Consortium, 2012). This claim was widely criticized (Rands et al., 2014, and references therein).

[11] Ironically, Lewontin, a harsh critic of adaptationism, and EP have come to the same conclusion via very different lines of reasoning. For EP, population genetic differences are unimportant because all humans share a universal, complex, genetically specified design that evolved, or was stabilized, in an African population over the last 2 million years.

[12] There also appears to be balancing selection at this locus (Ding et al., 2002).