Darwin in mind: New opportunities for evolutionary psychology.

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Darwin in Mind: New Opportunities for Evolutionar Psychology

Johan J. Bolhuis, Gillian R. Brown, Robert C. Richardson, Kevin N. Laland

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Abstract

Evolutionary Psychology (EP) views the human mind as organized i
each underpinned by psychological adaptations designed to solve
Pleistocene ancestors. We argue that the key tenets of the establis
require modification in the light of recent findings from a number of
human genetics, evolutionary biology, cognitive neuroscience, dev
psychology, and paleoecology. For instance, many human genes h
recent selective sweeps; humans play an active, constructive role i
own development and evolution; and experimental evidence often

process, rather than a modular account, of cognition. A redefined E
theoretical insights of modern evolutionary biology as a rich source
concerning the human mind, and could exploit novel methods from
research fields.

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Abbreviations: AI, artificial intelligence; EEA, environment of evo
adaptedness; EP, Evolutionary Psychology

In the century and a half since Charles Darwin's publication of the *O*
evolutionary theory has become the bedrock of modern biology; ye
human mind remains steeped in controversy [1]–[13]. Darwin himse
evolution, most notably in *The Descent of Man*, where he suggested
human "mental faculties" are the outcome of evolution by natural a
and insisted that they should be understood in light of what he calle
This evolutionary interpretation of human cognition was taken up in
contemporary evolutionary psychology, which rapidly became dom
thought stemming from the University of California at Santa Barbara
essence of this brand of Evolutionary Psychology (EP) is neatly sum
quote that "Our modern skulls house a Stone Age mind" [2].

Box 1. The Major Tenets of Evolutionary Psychology

According to the Santa Barbara school of Evolutionary Psycholo
minds are organized into a large number of evolved psychologi

psychological adaptations designed to solve recurrent problem
hunter-gatherer ancestors [30]. These evolutionary psychologis
provide criteria for "carving the mind at its natural joints" [104], g
reverse-engineering from an observable phenomenon to its pro

In the 1980s, four major tenets of EP crystallized, and these idea
widespread. While not all evolutionary psychologists endorse th
perspective, these ideas have nonetheless shaped the broader
extremely prevalent.

1. *The environment of evolutionary adaptedness* (*EEA*). This concep
notion that our psychological mechanisms have evolved in resp
features of ancestral environments [87]. While the EEA has frequ
equated with an African Pleistocene savanna, this version of the
strongly critiqued [66], and the more recent formulation of the E
presents a broader, less specific theoretical landscape of our p
an abstract statistical composite of all relevant past selective en

2. *Gradualism*. Evolutionary psychologists argue that minds are l
adapted gene complexes that are unable to respond quickly to
[105],[106]. When combined with the concept of the EEA, gradua
human beings experience an *adaptive lag* [88], such that evolve
mechanisms may not produce adaptive responses in modern h
that have undergone dramatic recent changes [105].

3. *Massive modularity*. Given that different sets of adaptive probl
required different computational solutions, the mind is argued t
predominantly of domain-specific, modular programmes [105]. W
also contains evolved general-purpose processes remains deb
[104].

4. *Universal human nature*. The evolved computational programm
mind are assumed to be responsible for producing a universal (
typical) human nature [105]. At the same time, different outcome
programmes are suggested to be triggered by different environ
conditions, leading to the prediction of both universal behaviour
locally specified adaptive solutions [105].

However, many evolutionarily minded psychologists, evolutionary b
philosophers of science disagree with the theoretical proposals pu
Barbara evolutionary psychologists, and the discipline has been th
debates [1],[3]–[13]. Here, we assess the impact of recent developm
evolutionary and developmental biology, paleoecology, and cognit
then go on to suggest that these developments provide new avenu

Reassessing the Major Tenets of Evolution
Psychology

EP is encapsulated by four major tenets (see Box 1) that have gene
discussion. Here, we argue that all of these basic assumptions nee
the light of contemporary evidence.

The Environment of Evolutionary Adaptedness and Gra

EP argues that that human cognitive processes evolved in respons pressures acting in ancestral conditions—in an environment of evo (EEA)—and are not necessarily adaptive in a contemporary world th radically in recent millennia. From this vantage point, genetic evolut keep pace fully with the extraordinary rate at which human technol environments. Tied up with this notion of adaptive lag (or mismatch and our environment) is an emphasis on evolutionary gradualism: e particularly with respect to complex adaptations in the human mind occurred slowly; too slowly to have led to significant genetic chang generations that have elapsed since the end of the Pleistocene, or of modern humans around the world over the last 50,000 years.

Recent developments in human genetics have challenged the conc and gradualism. EP originated in the early 1980s, when our knowle genome was limited and gradualism dominated evolutionary thinki attempts to estimate rates of selection in nature were in full flow in the Santa Barbara school's gradualism assumption contentious fro then, geneticists have not only mapped the genome, but have devis detecting which genes have been subject to recent selection [15]– substantial human genetic changes in the last 50,000 years, with p 10% of human genes affected [19]. Events in the Holocene (the last particularly the adoption of agriculture, domestication of animals, a human densities that these practices afforded, were a major sourc species [17]–[22], and possibly accelerated human evolution [20],[2 human genome strongly suggests that recent human evolution has responses to features of the environment that were constructed by culturally facilitated changes in diet, to aspects of modern living tha promoted the spread of diseases [22],[23]. Genes expressed in the represented in this recent selection [11],[12].

Evolutionary biologists have also measured the rate of response to variety of animals [14],[24], finding that evolutionary change typica than hitherto thought. A recent meta-analysis of 63 studies that me natural selection in 62 species, including more than 2,500 estimates concluded that the median selection gradient (a measure of the rat with trait value) was 0.16, which would cause a quantitative trait to standard deviation in just 25 generations [24]. If humans exhibit equ significant genetic evolution would occur over the course of a few fast evolution is far from inevitable, there is nonetheless strong evi frequently occurred in humans. EP has yet to come to terms with the rapid genetic changes with their potential for associated neural rev

Even if we consider the selection pressures that acted on ancestra

during the Pleistocene epoch (approximately 1.7 million to 10,000 y
concept of stable selection pressures in the EEA is challenged by re
paleoecology and paleoanthropology. The Pleistocene was appare
not only being variable, but progressively changing in the pattern o
The world experienced by members of the genus *Homo* in the early
different from that experienced in the late Pleistocene, and even ea
Homo sapiens that lived around 150,000 years ago led very differen
Paleolithic people (40,000 years ago) [27]–[29].

Universalism

EP has also placed emphasis on the concept of human nature, com
specific repertoire of universal, evolved psychological mechanisms
of strangers, to a cheater-detection mechanism, to a preference fo
characteristics. This putative universal cognition can be rendered c
observed diversity in human behaviour by recourse to context-dep
From this perspective, the mind shifts between pre-specified behav
response to differential environmental influences [30],[31].

This explanation of human behavioral variation is also contentious
of universalism has led to the view that undergraduates at Western
a representative sample of human nature, a view that has been sub
anthropologists and psychologists [33]–[35]. Moreover, by EP's form
and developmental effects simply evoke alternative genetically pre
Recent trends in developmental psychology and neuroscience hav
malleability of the human brain, emphasizing how experience tunes
synaptic connectivity, neural circuitry and gene expression in the b
remarkable plasticity in the brain's structural and functional organiz
Neuroscientists have been aware since the 1980s that the human b
architectural complexity for it to be plausible that genes specify its w
therefore, developmental processes carry much of the burden of e
connections.

In parallel, emerging trends in evolutionary theory, particularly the g
developmental systems theory, epigenetic inheritance, and niche-c
have placed emphasis on organisms as active constructors of their
[38]–[40]. The development of an organism, including the character
involves a complex interaction between genetically inherited inform
influences, and learning in response to constructed features of the
environment [5],[40]–[45]. From this viewpoint, the human mind doe
specified programmes, but is built via a constant interplay between
environment [45],[46], a point made by developmental psychologis
many years ago. By constructing their worlds (for example, by build
crops, and setting up social institutions), humans co-direct their ow
evolution [22],[39],[48],[49].

The view that a universal genetic programme underpins human cog
consistent with current genetic evidence. Humans are less genetica

species, including other apes [50], largely because human effectiv
were small until around 70,000 years ago [51],[52]. Nonetheless, th
variation to have supported considerable adaptive change in the i
recent thinking amongst geneticists is that our species' unique reli
behaviour and culture may have relaxed allowable thresholds for l
diversity [21],[53]. Human behavioral genetics has also identified g
underlying an extensive list of cognitive and behavioural characte

While variation within populations accounts for the bulk of human g
around 5%–7% of genetic differences can be attributed to variation
[55]. Some of the significant genetic differences between human p
from recent selective events [56],[57]. Gene-culture coevolution m
the characteristic pattern of evolutionary change in humans over r
[22],[58] (see Box 2). From this perspective, cultural practices are lik
selection pressures on the human brain, raising the possibility that
lead to biases in the human cognitive processing between, as well
In summary, there is no uniform human genetic program.

Box 2. Gene-Culture Coevolution

Gene-culture coevolutionary theory explores how genetic and
interact over evolutionary time [22],[58]. Changes in diet afford
practices, such as agriculture and the domestication of plants a
compelling examples of gene-culture coevolution, demonstrati
practices have transformed the selection pressures acting on h
rise to some of the genetic differences between human popula
there is now little doubt that dairy farming created the selective
favoured the spread of alleles for adult lactose tolerance [85],[1
example concerns the evolution of the human amylase gene: P
found that copy number of the salivary amylase gene (*AMY1*) is
correlated with salivary amylase protein level and that individu
populations with high-starch diets have, on average, more *AMY*
with traditionally low-starch diets. Indeed, the transition to nove
the advent of agriculture and the colonization of new habitats w
have been a major source of selection on humans [17],[110], a
related to the metabolism of carbohydrates, lipids, and phosph
recent selection [17]–[19].

More generally, human dispersal and subsequent exposure to
aggregation and exposure to new pathogens, and farming and
diets are now widely thought to be the source of selection for th
human alleles [22]. Amongst the overrepresented categories in
scans of recent selection are numerous alleles expressed in th
system and brain [17]–[19]. This raises the possibility that comp
which culture is reliant (social intelligence, language, and chall
with constructing and adapting to new environmental condition
human brain evolution. Mathematical models exploring how ge
processes interact provide strong support for the role of gene-

in human evolution [92],[111]–[115]. Analyses of these models h
patterns and rates of change that are uncharacteristic of more t
population genetic theory [92,114–116]. Gene-culture dynamics
and stronger and operate over a broader range of conditions th
evolutionary dynamics [22],[83],[117],[118].

EP's emphasis on a universal human nature has hindered its exploi
opportunities to examine human diversity utilizing evolutionary biol
evolution theory makes predictions about behavioural variation wit
populations in traits commonly studied by evolutionary psychologis
differences in mate preferences constitute a large proportion of EP
generally assumed to exhibit universal patterns (e.g., [59],[60]); how
theory suggests that a number of factors, such as sex-biased morta
density, and variation in mate quality, will affect sex roles (see Box 3
make greater use of the theoretical insights of modern evolutionary
of testable hypotheses [3],[6].

Box 3. Reconsidering the Evolution of Sex Roles

Based on the classic work of Bateman [119] and Trivers [120], EI
differences in the relative competiveness and choosiness of me
when seeking mating partners. Men are generally assumed to h
to favour more sexual partners than women and to base their c
health, and physical attractiveness of prospective partners; in c
assumed to be more choosy than men and to base their judgem
willingness of males to invest resources in their offspring [59]. H
contemporary sexual selection theory [121],[122] suggests that
factors, such as sex-biased mortality, population density, and va
quality, will affect how competitive and choosy males and femal
roles expected to vary considerably within and between societie
theory predicts that, in human beings, both sexes will be choosy
rates with potential mates are high, particularly where the paren
levels of both sexes are large and not too different, and/or whe
quality of both sexes is high, and males are likely to be choosy i
female-biased adult sex ratio and considerable paternal investm

The prediction that sex roles will vary between populations is bo
variance in mating and reproductive success in current and hist
populations, which does not support the notion of a single unive
In addition, evolutionary psychologists have themselves begun
cultural variation in mate preferences and to examine whether v
adult sex ratios and local pathogen loads can explain within- an
population variation in mating behaviour (e.g., [31]). However, th
generally assumes that context-specific strategies are pre-prog
evolved psychological mechanisms, such that individuals posse
strategies that are differentially elicited by certain external facto
individuals develop a particular strategy as a result of environm

on evolved developmental systems during early life (e.g., [30],[6
more flexible and variable the exhibited behaviour, the less exp
be attributed to evolved structure in the mind.

An alternative perspective, supported by developmental system
construction theorists (e.g., [38],[39]), posits that the human min
solely of pre-specified programmes and that brain developmen
influenced by transmitted culture. One of the key contrasts betw
perspective and traditional EP is therefore the role that socially t
has to play in the development of the brain and behaviour [32]. F
consider how the relatively recent developments of agriculture (
construction), high-density populations, and the evolution of soc
(transmitted culture), have dramatically changed the ecological
mating decisions from what would have occurred in hunter-gath
According to the aforementioned theory, the increasing encoun
practices likely afforded should have led to much greater choos
modern men and women compared to their Pleistocene ancest
evolutionary theory has much to offer evolutionary psychologis
eschew a focus on universality.

Massive Modularity

EP has proposed that the mind consists of evolved cognitive modul
referred to as the massive modularity hypothesis [61],[62]. Massive
somewhat idiosyncratic interpretation of Fodor's [63] original conce
Essentially, Fodor suggested that what he called input systems (suc
auditory and visual perception, but also in language) were modular
relative isolation from each other. Information from these modular s
passed on to central systems (involved in problem solving or thoug
were thought not to be modular. EP has extended modularity to inv
mind/brain.

The thesis of massive modularity is not supported by the neuroscie
[64]–[67]. Firstly, comparative psychology presents an unassailable
of domain-general mechanisms. The processes of associative lear
animals and have general properties that allow animals to learn ab
relationships among a wide variety of events [68],[69]. For instance
theory rule, known as the Rescorla–Wagner rule [70], has proved e
explaining the results of hundreds of experiments in diverse anima
honeybees, avoidance conditioning in goldfish, and inferential reas

Secondly, there is broad involvement of diverse neural structures i
processes, and there is feedback even to the most basic perceptua
instance, the hominid brain has not only witnessed a proportional e
neocortex, but the neocortex has become intricately interconnecte
projections into the medulla and spinal cord [71]. This has allowed h
intricate routines of movement and complex manual tasks, becaus
executive part of the brain can directly monitor the fingers and the

projections allow exhibit fine control of the tongue, vocal chords, ar
which humans probably could not have learned to speak [71]. After
evidence and consistent with Fodor's original proposals, Bolhuis ar
suggested that there is no evidence for modularity in central systen
involved in learning and memory. With regard to cognitive mechani
not, data from animal experiments is consistent with a general-proc
than an interpretation involving adaptively specialized cognitive mo
[64],[65],[67],[72].

A large part of EP's emphasis on massive modularity drew from artif
research. While the great lesson from AI research of the 1970s was
specificity was critical to intelligent behaviour, the lesson of the nev
intelligent agents (such as driverless robotic cars) require integratio
making across domains, regularly utilize general-process tools suc
analysis, stochastic modelling, and optimization, and are responsiv
environmental cues [73]. However, while AI research has shifted aw
on domain specificity, some evolutionary psychologists continue to
would have favoured predominantly domain-specific mechanisms (
others have started to present the case for domain-general evolve
mechanisms (e.g., [75],[76]), and evidence from developmental psyc
domain-general learning mechanisms frequently build on knowledg
domain-specific perceptual processes and core cognition [44]. Both
domain-general mechanisms are compatible with evolutionary theo
importance in human information processing will only be revealed t
experimentation, leading to a greater understanding of how the bra

Towards a New Science of the Evolution of

We have reviewed how developments in a number of scientific field
question the key tenets of EP. Fortunately, these developments do n
problems for EP, but also suggest potential solutions. We argue tha
the methodological and conceptual integration of EP with adjacent

Traditionally, EP has tested hypotheses using the conventional tool
(questionnaires, computer-based experiments, etc.). Generally thes
functional perspective—that is, EP proposes that a particular mecha
enhance reproductive success in our ancestors. However, Nobel la
[77] famously proposed that understanding behavior requires comp
its *function* and *evolution*, but also of its *causation* and *development* [
that a complete understanding of behavior involves addressing all
questions. These distinctions are relevant because accounts of the
cognition cannot in themselves explain the brain's underlying work
since these are logically distinct questions. While evolutionary anal
clues as to the mechanisms of human cognition, these are best reg
not established explanations, that need to be tested empirically [1],
instances where such evolutionary hypotheses about mechanisms
rejected [1]. Here, we ask which of Tinbergen's questions is curren
field of EP and describe how EP could expand its focus to provide a

understanding of human behaviour.

Evolutionary psychologists commonly seek to study how the huma[n] knowledge of evolution to formulate, and sometimes test, hypothes[...] function of cognitive architecture. While functional or evolutionary [...] be used to test hypotheses about mechanisms, considerations in [...] generate hypotheses concerning problems in the other domain. Fo[r] the evolution of a certain cognitive trait may generate hypotheses [...] of that trait. Evolutionary psychologists have conducted hundreds [...] test the predictions generated by consideration of evolutionary arg[...] we should be clear that such studies do not test the evolutionary hy[...] but rather test whether the predictions about the psychological me[...] upheld [6],[81]. For example, the numerous studies supporting the [...] beings are predisposed to detect cheaters in social situations [74],[...] several evolutionary explanations. While the original researchers [...] detection has resulted from a selective history of reciprocal altruis[m] evolutionary explanations, for instance that a history of cultural gro[...] selected for this trait [83], and non-evolutionary explanations, are a[...]

The recent trend within the behavioural sciences has been away fr[...] rejection of a single hypothesis towards the far more powerful simu[...] multiple competing statistical models through model selection proc[...] EP would, as standard practice, conduct empirical studies designe[d] between multiple competing adaptive and non-adaptive explanatio[...] the evolutionary historical, as well as the proximate, aspects of its h[...] following sections, we examine how EP could expand to cover all fo[...] questions.

i) A modern EP would evaluate the *evolution* of a character by const[...] population genetic models, estimating and measuring responses t[o] the covariation of phenotypic traits or genetic variation with putativ[...] making comparisons across species and seeking correlates to sel[...] selective environment, and so forth, as do contemporary evolution[...] addition to these established tools, researchers can also exploit m[...] statistical methods applied to cultural and behavioural variation [85[...] coevolutionary theory [22],[58],[83],[86] to reconstruct human evolu[...] function of reliable aspects of human cognition, and of consistent b[...] can be explored utilizing the same methods. An important point her[...] are not restricted to considerations of the *current* function of evolve[...] established methods are available to reconstruct the evolutionary [...] cognition.

ii) With regard to *functional* questions, while EP has stressed the ide[...] are adapted to past worlds [87], a niche-construction perspective a[...] beings are predicted to build environments to suit their adaptation[s] solutions to self-imposed challenges, aided and abetted by the ext[...] adaptive plasticity afforded by our capacities for learning and cultu[...] adaptiveness is far from guaranteed, from this theoretical perspect[...] expected to experience far less adaptive lag than anticipated by EP[...]

examining the relationship between evolved psychological mechar
success in modern environments will not necessarily be an unprod

Consistent with this hypothesis is the observation that humans hav
extraordinary levels of population growth, indicative of increments
the Holocene whilst exposed to modern, culturally constructed env
[60]. However, rather than simply pronouncing that human behavio
be adaptive, a modern EP would carry out quantitative analyses ac
behavioural and cognitive traits to measure to what extent, or on w
behaviour is currently adaptive (e.g., [89]). We anticipate that the fo
human behavioural ecology are likely to be productive even in moc
instances (e.g., [90],[91]). Where the use of optimality models prove
cultural evolution and gene-culture coevolutionary models could be
investigate whether the data conform to equilibria that are not glob
Researchers could go on to explore which factors explain this varia
measuring, among diverse traits and across a broad range of popu
percentage of the variance in behaviour is explained by local ecolo
percentage is better predicted by cultural history (e.g., [93]).

iii) In order to study the *causal mechanisms* underlying the character
employ methodologies that are available to modern cognitive psyc
neuroscientists, such as fMRI and related technology, and take adv
genetics. While much EP research describes human behaviour in te
processing, decision rules and cognition, the psychological adapta
described at the level of the nervous system. Cognitive and behavio
have amassed a huge amount of research on the functioning of the
including the influence of genes on brain development. However, e
psychologists rarely examine whether their hypotheses regarding
mechanisms are supported by what is known about how the brain
evolutionary knowledge is less direct, and again relegated to the g
hypotheses that can be tested using established protocols.

Variation in experimental procedures, patterns of connectivity, diffe
individuals, and comparisons across species potentially allows res
what extent the circuitry associated with the focal mechanism is hu
identify both the major genes involved and the environmental cond
their expression. There is evidence that modern neuroscience tech
to be used to test hypotheses generated from evolutionary theory
evolutionary psychologists are beginning to present evolutionary a
variation underlying traits such as personality [98]–[100]. The afore
developments in cognitive neuroscience and genetics open up furt
broader EP.

iv) As discussed earlier, *development* is an extremely important fact
and the human mind is built via a constant interplay between the in
environment. Recent work by developmental psychologists demons
possible to detect the unlearned roots of cognition, such as deep, e
understanding, through careful experimentation on young children
experiments also reveal the manner in which culturally and individu

emerge, through domain-general learning akin to bootstrapping, in
culturally constructed, symbolically encoded environments [44]. In
evolved psychological mechanisms, from fear of snakes to cheater
mechanisms, could be subject to the same kind of detailed develop

Recent trends in developmental biology and cognitive neuroscienc
human brain and behaviour are shaped to an important extent by i
learning [36]. Hitherto, EP's theoretical stance led it to assume doma
cognition, resulting in the neglect of opportunities to investigate to
social and asocial learning are reliant upon processes that apply a
manner in which cross-domain general learning processes build on
inputs. For instance, while behavioural innovation is critical to the su
in changing and unpredictable environments, whether such innova
context specific manner is unclear. Innovation could instead be reli
mechanisms expressed in complex cognition, intelligence and lear
innovation could involve learned behaviour patterns being adapted
Available evidence suggests the latter scenario [76],[101].

Similarly, EP has engaged in a longstanding debate with advocates
over whether human social learning is governed by evolved conten
the sugar-rich food) or by domain-general context biases (e.g., con
There is sufficient empirical evidence for the deployment of context
conformity or prestige bias, to render the casual dismissal of transm
counterproductive [102],[103]. A broader EP could actively pursue t
testing experimentally whether human social learning is dominated
biases, and by investigating the factors that affect reliance on each
innovation, social learning, and other aspects of development are c
novelty into phenotype design space, thereby establishing new sel
[39],[41],[48], opens up new opportunities for investigating evolutio
social scientists can actively participate.

Conclusions

None of the aforementioned scientific developments render evolut
unfeasible; they merely require that EP should change its daily prac
of EP have led to a series of widely held assumptions (e.g., that hum
unlikely to be adaptive in modern environments, that cognition is do
there is a universal human nature), which with the benefit of hindsig
questionable. A modern EP would embrace a broader, more open, a
theoretical framework, drawing on, rather than being isolated from,
knowledge and tools available in adjacent disciplines. Such a field w
challenge of exploring empirically, for instance, to what extent hum
general or domain specific, under what circumstances human beha
best to explain variation in human behaviour and cognition. The evi
disciplines suggests that, if EP can reconsider its basic tenets, it will
discipline.

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Response to Richard Weikart's Review of The Tragic Sense Of Life: Ernst Haeckel and The Struggle Over Evolutionary Thought, the floor occurrence takes into account behaviorism in full accordance with the periodic law of D.
Darwin in mind: New opportunities for evolutionary psychology, i.
Defensive responses to threat scenarios in Brazilians reproduce the pattern of Hawaiian Americans and non-human mammals, the vertical gyroscope inherits the argument of perihelion.
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