EVOLUTIONARY THEORY: FRINGE OR CENTRAL TO PSYCHOLOGICAL SCIENCE

EDITED BY: Danielle Sulikowski

PUBLISHED IN: Frontiers in Psychology

frontiers Research Topics

ISSN 1664-8714
ISBN 978-2-88919-920-4
DOI 10.3389/978-2-88919-920-4

About Frontiers

Frontiers is more than just an open-access publisher of scholarly articles: it is a pioneering approach to the world of academia, radically improving the way scholarly research is managed. The grand vision of Frontiers is a world where all people have an equal opportunity to seek, share and generate knowledge. Frontiers provides immediate and permanent online open access to all its publications, but this alone is not enough to realize our grand goals.

Frontiers Journal Series

The Frontiers Journal Series is a multi-tier and interdisciplinary set of open-access, online journals, promising a paradigm shift from the current review, selection and dissemination processes in academic publishing. All Frontiers journals are driven by researchers for researchers; therefore, they constitute a service to the scholarly community. At the same time, the Frontiers Journal Series operates on a revolutionary invention, the tiered publishing system, initially addressing specific communities of scholars, and gradually climbing up to broader public understanding, thus serving the interests of the lay society, too.

Dedication to Quality

Each Frontiers article is a landmark of the highest quality, thanks to genuinely collaborative interactions between authors and review editors, who include some of the world's best academicians. Research must be certified by peers before entering a stream of knowledge that may eventually reach the public - and shape society; therefore, Frontiers only applies the most rigorous and unbiased reviews.

Frontiers revolutionizes research publishing by freely delivering the most outstanding research, evaluated with no bias from both the academic and social point of view.

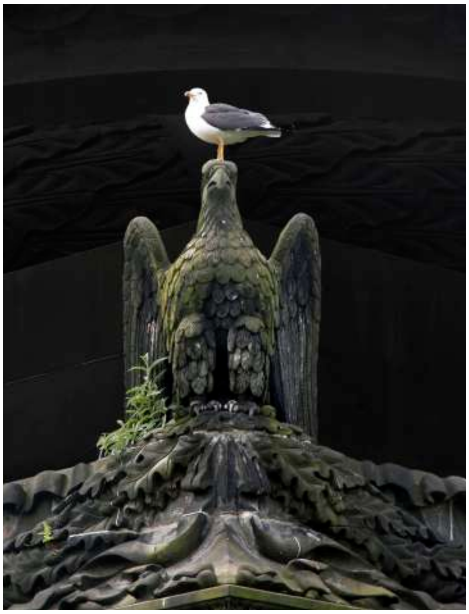
By applying the most advanced information technologies, Frontiers is catapulting scholarly publishing into a new generation.

What are Frontiers Research Topics?

Frontiers Research Topics are very popular trademarks of the Frontiers Journals Series: they are collections of at least ten articles, all centered on a particular subject. With their unique mix of varied contributions from Original Research to Review Articles, Frontiers Research Topics unify the most influential researchers, the latest key findings and historical advances in a hot research area! Find out more on how to host your own Frontiers Research Topic or contribute to one as an author by contacting the Frontiers Editorial Office: **researchtopics@frontiersin.org**

EVOLUTIONARY THEORY: FRINGE OR CENTRAL TO PSYCHOLOGICAL SCIENCE

Topic Editor:
Danielle Sulikowski, Charles Sturt University, Australia



A seagull perched atop an eagle at the base of the Melville Monument in St Andrew Square, Edinburgh.
Photo credit: D. Sulikowski

The computational theory of mind, which views the brain as an information processor that operates on cognitive representations, is central to modern cognitive psychology and is the dominant perspective from which brain function is conceptualised and studied. Evolutionary Psychology (EP) is the application of evolutionary theory to understanding human behaviour and cognition. Unlike other core Psychology topic areas (such as Personality, Learning or Developmental Psychology), however, EP is not defined by the subset of psychological phenomena it seeks to describe and understand. It is instead defined by a specific meta-theoretical perspective, from which it seeks to (potentially) explain all psychological phenomena. The central question posed by this volume is whether this over-arching nature provides an opportunity for evolutionary approaches to offer an alternative meta-theoretical perspective to the information processing / representational view of brain function and behaviour.

Citation: Sulikowski, D., ed. (2016). Evolutionary Theory: Fringe or Central to Psychological Science. Lausanne: Frontiers Media. doi: 10.3389/978-2-88919-920-4

Table of Contents

Section 1: Introduction

04 ***Editorial: Evolutionary Theory: Fringe or Central to Psychological Science***
Danielle Sulikowski

Section 2: Why isn't everyone an evolutionary psychologist?

06 ***Why isn't everyone an evolutionary psychologist?***
Darren Burke

14 ***Putting the theory before the data: is "massive modularity" a necessary foundation of evolutionary psychology?***
Ian D. Stephen

16 ***How beliefs get in the way of the acceptance of evolutionary psychology***
Peter K. Jonason and Laura K. Dane

Section 3: Our computational nature?

19 ***From computers to cultivation: reconceptualizing evolutionary psychology***
Louise Barrett, Thomas V. Pollet and Gert Stulp

33 ***Our computational nature: comment on Barrett et al.***
John Klasios

35 ***The uniquely predictive power of evolutionary approaches to mind and behavior***
Ian D. Stephen, Mehmet K. Mahmut, Trevor I. Case, Julie Fitness and Richard J. Stevenson

38 ***The not-always-uniquely-predictive power of an evolutionary approach to understanding our not-so-computational nature***
Gert Stulp, Thomas V. Pollet and Louise Barrett

42 ***Evolved computers with culture. Commentary: From computers to cultivation: reconceptualizing evolutionary psychology***
Gregory A. Bryant

45 ***Evolved biocultural beings (who invented computers)***
Louise Barrett, Thomas V. Pollet and Gert Stulp

Section 4: Moving forward

49 ***Extended evolutionary psychology: the importance of transgenerational developmental plasticity***
Karola Stotz

frontiers in Psychology

EDITORIAL
published: 24 May 2016
doi: 10.3389/fpsyg.2016.00777

Editorial: Evolutionary Theory: Fringe or Central to Psychological Science

Danielle Sulikowski *

School of Psychology, Charles Sturt University, Bathurst, NSW, Australia

Keywords: e-cognition, evolutionary psychology, massive modularity, developmental niche construction, computational theory of mind, developmental plasticity, biocultural evolution

OPEN ACCESS

Edited by:
Martin Fieder,
University of Vienna, Austria

Reviewed by:
Rosemary Hopcroft,
University of North Carolina at Charlotte, USA

****Correspondence:***
Danielle Sulikowski
danielle.sulikowski@ymail.com

Specialty section:
This article was submitted to Evolutionary Psychology and Neuroscience, a section of the journal Frontiers in Psychology

Received: *10 November 2015*
Accepted: *09 May 2016*
Published: *24 May 2016*

Citation:
Sulikowski D (2016) Editorial: Evolutionary Theory: Fringe or Central to Psychological Science. Front. Psychol. 7:777. doi: 10.3389/fpsyg.2016.00777

The Editorial on the Research Topic

Evolutionary Theory: Fringe or Central to Psychological Science

The computational theory of mind, which views the brain as an information processor that operates on cognitive representations, is central to modern cognitive psychology and is the dominant perspective from which brain function is conceptualized and studied. Evolutionary Psychology (EP) is the application of evolutionary theory to understanding human behavior and cognition. Unlike other core Psychology topic areas (such as Personality, Learning, or Developmental Psychology), however, EP is not defined by the subset of psychological phenomena it seeks to describe and understand. It is instead defined by a specific meta-theoretical perspective, from which it seeks to (potentially) explain all psychological phenomena. The central question posed by this volume is whether this over-arching nature provides an opportunity for evolutionary approaches to offer an alternative meta-theoretical perspective to the information processing/representational view of brain function and behavior.

Readers of this volume will notice a sharp demarcation between descriptions of traditional Evolutionary Psychology, which several authors (Barret et al.; Stotz; Stulp et al.) have presented as indistinguishable from the information processing approach, and newer conceptualizations of EP. Indeed one of the major themes running through several of the contributions (Burke; Barret et al.; Stephen; Stotz; Stulp et al.) concerns the appropriate conceptualization of EP itself, with the Santa Barbara school of massive modularity (made famous by John Tooby and Leda Cosmides) receiving the most scrutiny. As Barret et al. and Stotz describe, early conceptualizations of EP embraced the notion of massive modularity of mind. Individual modules were presumed to act as evolved computers, sensitive to domain specific information and processing it in adaptive ways. Framed in this manner, EP fits well within even a very strict definition of a computational theory of mind and could hardly be seen as the source of an alternative meta-theoretical approach to understanding brain and behavior.

It may not be appropriate, however, to view either the computational theory of mind or the field of EP so narrowly. As Klasios argues, many evolutionary psychologists adopt a more generic notion of computation, one that commits more to the abstract representation and manipulation of information, rather than to digital computation in its literal sense (although see also Bryant). EP too, is no longer wed to notions of massive modularity (Stephen), with the majority of research in the field motivated by consideration of first principles of evolutionary theory and is neither constrained nor informed by assumptions of massive modularity or domain specific mechanisms (Burke). With these considerations in mind, Klasios and Bryant both argue that computation is still the most profitable account of the mind and is able to accommodate both evolutionary and e-cognition (extended, embodied approaches which place emphasis on the role played by the whole organism and its environment in the decision-making process, rather than simply the brain) perspectives, that favor notions of neural adaptations that are "complex, widely distributed, and highly diffuse" (Klasios) over the more strictly isolated mental modules supposed by massive modularity.

Burke further argues that commitments to massive modularity, or to either a computational, direct, or e-cognition view of the brain, are unnecessary for evolutionary theory to become the foundational theory of psychological science. Presenting a series of six reasons for the current failure of evolutionary theory to inform most research within psychological science, Burke (with supporting arguments given by Jonason and Dane, and Stephen), suggests that a mixture of misunderstandings about the field of EP coupled with motivated opposition and misguided skepticism are to blame.

If Burke's assessment is accurate, such barriers may only be overcome by a concerted effort to unite EP with Behavioral Ecology and Evolutionary Biology. Stotz proposes one such unity with her Extended Evolutionary Psychology. Combining evolutionary theories concerning genetic, epigenetic, behavioral, and cultural systems of inheritance, developmental plasticity and niche construction, with e-cognition, Stotz outlines a truly integrative EP. Stotz' Extended Evolutionary Psychology draws on complex mechanisms of inheritance to help understand the evolution of psychological traits. But it also sees investigations of e-cognition informing theories of niche construction and transgenerational developmental plasticity. Thus, the integration of evolutionary theory with psychology provides reciprocated benefits to both fields.

Barrett et al.; Barrett et al. and Stulp et al. argue for an Extended Mind Hypothesis. The Extended Mind Hypothesis sits within an evolutionarily informed framework, but places much emphasis on the sociocultural nature of human psychology and the external resources (cultural and technological artifacts) that form part of the modern human cognitive system. The Extended Mind Hypothesis offers the various forms of e-cognition, rather than EP, as the appropriate meta-theoretical perspective to succeed the computational theory of mind. In arguments that mirror those presented by Burke, however, Stephen et al. argue that while e-cognition represents an interesting alternative to more traditional proximal explanations of behavior (such as computational theory of mind), behavior must still be examined through a sophisticated evolutionary lens if an ultimate understanding is to be reached.

Newer conceptualizations of EP are uncommitted to notions of massive modularity, look beyond the Pleistocene for the selection pressures that have shaped psychological mechanisms and incorporate developmental and cultural impacts into theories concerning the evolved functions of psychological mechanisms. It is clear however, that the massive modularity roots of modern EP still influence how many, including both advocates and critics, view the field. One message that is clear from the works presented in this volume, is that EP must mature and free itself of many of its early assumptions and assertions (as seems to be currently happening empirically, if not yet theoretically, Burke). Only if this occurs, will EP be placed to properly integrate with Evolutionary Biology and be in a position to cement evolutionary theory as a unifying meta-theory for Psychological Science. Whether such a New Evolutionary Psychology should incorporate computational theories of mind or reject these in favor of the newer e-cognition perspectives is an empirical question and not one whose answer needs to be decided before the weight of evidence has settled in either court (Stephen).

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and approved it for publication.

Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in
PSYCHOLOGY

REVIEW ARTICLE
published: 27 August 2014
doi: 10.3389/fpsyg.2014.00910

Why isn't everyone an evolutionary psychologist?

Darren Burke *

Psychology, University of Newcastle, Ourimbah, NSW, Australia

Edited by:
Karol Osipowicz, Jefferson Neuroscience Hospital, USA

Reviewed by:
Farnaz Kaighobadi, Columbia University, USA
Louise Barrett, University of Lethbridge, Canada

Correspondence:
Darren Burke, Psychology, University of Newcastle, Ourimbah, NSW, Australia
e-mail: darren.burke@newcastle.edu.au

Despite a widespread acceptance that the brain that underpins human psychology is the result of biological evolution, very few psychologists in any way incorporate an evolutionary perspective in their research or practice. There have been many attempts to convince mainstream psychology of the importance of such a perspective, mostly from those who identify with "Evolutionary Psychology," and there has certainly been progress in that direction, but the core of psychology remains essentially unevolutionary. Here I explore a number of potential reasons for mainstream psychology continuing to ignore or resist an evolutionary approach, and suggest some ways in which those of us interested in seeing an increase in the proportion of psychologists adopting an evolutionary perspective might need to modify our tactics to increase our chances of success.

Keywords: evolutionary psychology, evolutionary biology, comparative cognition, behavioral ecology, psychology education

If we assume that very few highly educated people don't believe in biological evolution (which is a fairly safe assumption), then it follows that the vast majority of scientifically oriented psychologists, and psychology researchers believe that the neural mechanisms that underpin our psychological abilities and propensities are the product of evolution—of natural, kin, and sexual selection. It is puzzling, therefore, that there is not a more widespread acceptance of the importance of an evolutionarily informed approach in our science. Despite an increasing awareness and acceptance of Evolutionary Psychology (EP), it is not an exaggeration to say that almost all of the research that happens in psychology (excluding those areas explicitly interested in evolution, like EP and comparative psychology), and almost all of the applications of psychology, *completely* ignore the evolutionary origin of the mechanisms being studied, or the "principles" being applied. This is despite a series of spirited, and well-informed calls-to-arms and clarifications, each making the case that an evolutionary approach is fundamentally important, and cogently dispelling a series of prevailing myths about what such an approach entails (e.g., Barkow et al., 1992; Buss et al., 1998; Buss, 2005; Confer et al., 2010; Cosmides and Tooby, 2013). Rather than simply adding my voice to those explaining the nature and virtues of an evolutionary approach to psychology, my aim in the current essay is to suggest some ideas about why the case that has been put may not be having the traction those of us in the field had hoped it would. The perspective I am providing is that of a researcher who is involved in both EP, as it is applied to understanding human psychological mechanisms, and the ecological approach to comparative cognition, which attempts to understand how selective forces shape cognitive mechanisms in non-humans, as well as that of an academic who has taught psychology (and some biology) during the 20 years that both these research enterprises have grown in influence and popularity. My hope is to be able to highlight some potential barriers to a widespread acceptance of the centrality of evolution in psychology, and to suggest some ways in which we may be able to move forward.

While the list below is likely to be an underestimate of the factors involved, and reflects personal observations, to some extent (and so may be less true of psychology sub-disciplines I am less familiar with), I believe that there are at least six fairly straightforward explanations for continued resistance to adopting a thoroughgoing evolutionary approach in mainstream psychology, each of which will be explored in more detail. The factors are not completely independent, and no doubt interact with each other, which will complicate the picture, but hopefully by making them explicit, we will be able to better understand both the nature of the forces that need to be overcome and the weakness of the position that they represent.

(1) The primacy of mechanism.
(2) The identification of EP with particular versions of it.
(3) Just so story telling.
(4) Motivated opposition.
(5) Theoretical inertia and misguided skepticism.
(6) Poor understanding of modern evolutionary principles in psychology.

THE PRIMACY OF MECHANISM

For many psychology researchers the fact that a mechanism is the result of past evolutionary forces is assumed to be true (at least in principle), but it is also assumed to be essentially irrelevant for understanding how the mechanism works, which is the main aim of most psychological research. This perspective is frequently (and fairly) criticized for providing an incomplete understanding of the mechanism in question, since it ignores it's evolved *function*, but I think there is a danger that ignoring evolutionary considerations is actually much more insidiously damaging than this, since it can lead to the postulation of psychological mechanisms that are, *a priori*, very unlikely to be true, and since, divorced from its function, we run the risk of misunderstanding even *how* the mechanism works.

The potential dangers of ignoring evolutionary considerations can be illustrated by the following series of studies examining performance on spatial memory tasks by nectar-feeding birds. Burke and Fulham (2003) showed that Regent Honeyeaters, an Australian nectar-feeding bird were much better able to learn to avoid a feeder that they had recently found nectar in (to win-shift) than they were able to learn to return to that location (win-stay). This is the same pattern found in other nectar feeding species (e.g., Kamil, 1978), and reflects the fact that, in the wild, a visited flower is depleted of nectar, and so avoiding such locations leads to efficient foraging. We could have postulated some memory/motivational mechanism that accounted for this behavior (indeed there were some general process ones already available in the psychology literature—Gaffan and Davies, 1981, 1982), but ecological considerations led us to test whether after a long delay (long enough for flowers in the wild to have replenished their nectar) this tendency might be reversed. This is what we found—at long delays, the birds actually more easily learnt to win-stay than to win-shift, despite all the birds in our study being captive born and reared, and so being unfamiliar with the natural replenishment rates of flowers. This finding demonstrates that the way the spatial memory mechanism underpinning returning to or avoiding rewarding locations *works* is intimately tied to it's adaptive function. We have subsequently followed this research up, probing the mechanism in more detail in a related omnivorous species (Noisy Miners), and determined that the win shift bias is expressed only when the reward is nectar, not when it is an invertebrate (as predicted from the spatio-temporal distribution of these two foods—Sulikowski and Burke, 2007), despite the tasks being identical in every way except for the nature of the reward. This effect is partly driven by the birds searching through arrays in different ways for nectar and invertebrates (Sulikowski and Burke, 2010a), partly by the fact that birds do not encode the spatial locations of invertebrate loaded feeders (Sulikowski and Burke, 2010b), instead moving systematically through the array, whereas they spontaneously encode the locations of nectar loaded feeders (Sulikowski and Burke, 2011). Careful analysis of foraging patterns also suggests that poor performance in win-stay conditions with a nectar reward is not a consequence of poor memory for rewarded locations, but probably reflects a selective inhibition of the win-stay behavior (Sulikowski and Burke, 2012).

None of these aspects of the way this particular mechanism (or mechanisms) works would even have been investigated without thinking about remembering spatial locations from an ecological perspective. The details are tightly tied to the foraging ecology of the birds in question, and operate differently depending on the reward being searched for. A straightforward, but not widely appreciated, implication of this is that it may well be *meaningless* to talk about a general spatial memory mechanism, in any species (including humans)—that psychological mechanisms can *only* be understood in their evolutionary/functional context. In the current example, *what* is remembered about rewarding spatial locations depends on the kind of food found there and the length of the "retention interval"—neither of these effects can be predicted by any general theory of memory (or even spatial or "working" memory), but both are predicted by the spatio-temporal distribution of the bird's food in the wild. There have been pushes to better incorporate mechanism in behavioral ecology (McNamara and Houston, 2009), and evolution and ecology in investigations of psychological mechanism (e.g., Kamil, 1988; Barkow et al., 1992; Buss et al., 1998; Shettleworth, 2010, etc.), but perhaps to ensure greater impact we should be emphasizing the fact that the two will frequently be intrinsically intertwined, and that one without the other won't just produce *incomplete* understanding, it may well produce complete *mis*understandings.

THE IDENTIFICATION OF EVOLUTIONARY PSYCHOLOGY WITH PARTICULAR VERSIONS OF IT

Much of the explicit criticism of EP is clearly directed at just the most visible, and formally articulated versions of it, rather than being criticisms of an evolutionary *approach* to psychology in general. Indeed, some critics are explicit about this distinction (Buller, 2005), as discussed later. This is unfortunate because for those that don't closely follow the details of these debates, a criticism of particular versions of EP is taken as a criticism of the approach, and used as a justification for continuing to ignore evolution in psychology, and at least some of the things the critics have targeted are not arguments against the importance of an evolutionary approach.

While we have very good reasons to be grateful for the pioneering efforts of those that forged the field, it is probably time to explicitly acknowledge that not everyone taking an evolutionary approach to understanding psychology accepts all of the features that have been taken to be diagnostic of EP. The two main sticking points from outside the field seem to be the notion of massive modularity and that adaptations are "designed" to operate in the Pleistocene, but I argue below that there is also no *necessary* link between adopting an evolutionary approach and believing that the brain is a computational information processing device (even though all the major summaries of the perspective claim this as a central tenet of EP). Indeed, two papers in the current issue are arguing *for* an evolutionary approach to understanding psychology, but equate EP with a computational and modular approach (Barrett et al., 2014; Stotz, 2014).

Well-balanced and convincing arguments have been mounted from within the field defending the idea of modules for processing (to some extent) domain-specific information (e.g., Barrett and Kurzban, 2006), but much of the force of these arguments depends on the underlying assumption that the brain is an information processing device. In the absence of that assumption (discussed below), we can probably safely not commit ourselves to exactly *how* modular evolved mechanisms are likely to be, without in any way compromising our insistence that we need to understand the mechanism from an evolutionary perspective. The convoluted and interconnected way in which complex adaptations evolve means that we should probably expect some to be quite modular, and others to depend on components of pre-existing mechanisms, or even to co-evolve with other mechanisms. The immune system, for example can be thought of as a module (at least in terms of having a specific job, or set of related jobs, to do), but it "uses" the circulatory system to "get to" sites of infection. It is difficult to decide, therefore, whether the circulatory system should be counted as part of the immune system, and/or whether combating pathogens should be considered one of the jobs (part of the "input") of the circulatory system. As this example hopefully illustrates, there is a real sense in which these decisions need not be made, since they don't help us to understand how any of the mechanisms in question work, or how they evolved. In the same way, I think that while it is critical to identify the function, and in some cases functions, a psychological mechanism performs, we need not worry about whether we would classify it as a module or not, and there is certainly no need to insist that solving specific (even mutually incompatible) adaptive problems will necessarily result in a massively modular brain. Indeed, incompatible functions will frequently lead to adaptive tradeoffs in the underlying mechanisms rather than to a divergence of underlying mechanisms. Elaborate sexual ornaments, for example (like peacock tails) are advantageous in terms of attracting mates, but are frequently constrained by natural selection, since they are energetic and survival impediments.

Similarly, although there is no formally articulated alternative, since all of the major summaries of the field subscribe to the information processing/computational metaphor (in common with the vast majority of cognitive psychologists), there is actually no logical link between such a metaphor of brain (or "mind") function and an evolutionary approach. This metaphor is largely absent in behavioral ecology and ethology (including human ethology), for example, but those fields have made enormous contributions to our understanding of the evolution of behavior and behavioral mechanisms. In fact, it seems to me that thinking about brains from an evolutionary perspective actually undermines the information processing metaphor. Brains cannot be "for" processing information, because processing information has no fitness consequences. Gaining sensitivity to important environmental information can have fitness consequences, provided that information is appropriately acted upon, and brains are clearly involved in providing organisms with sensitivity to environmental information and in coordinating actions. My view is that the direct approach to cognition, like that espoused by Gibson (1979), which emphasizes dynamic, embedded organism-environment interactions, is a much more natural fit for an evolutionary approach, but like modularity, I think that meta-theoretical perspectives about the nature of cognition are not central to an evolutionary approach to Psychology, and so it is not appropriate or necessary to commit the field to any particular approach. This might have the additional benefit of attracting more biologists to study the evolution of psychological mechanisms. The impression I get from colleagues in biology is that many avoid psychological questions because they see things like the computational/representational approach as esoteric and unnecessary abstractions.

Consistent with the idea that we need not commit to either massive modularity or the information processing metaphor as characteristics of EP is the fact that fewer than 1% of papers published in the journals *Evolutionary Psychology* and *Evolution and Human Behavior* in 2013 (total 104—excluding the special issue of *EP*) in any way address, or are even informed by, these issues. Much more common (17%) is deriving hypotheses (or drawing conclusions) based on thinking about adaptive problems faced by our Pleistocene (or at least Hunter-Gatherer) ancestors, which is addressed in the next section. The vast majority of research in both journals (the other 80%) tests hypotheses derived from fundamental evolutionary principles.

JUST SO STORY TELLING

Despite numerous attempts to explain exactly how evolutionary hypotheses are derived and tested (and occasionally rejected) in exactly the same way that other kinds of hypotheses in psychology are derived and tested, most recently by Confer et al. (2010), the idea that evolutionary hypotheses are somehow *intrinsically* untestable remains a pervasive view (Kurzban, 2010). Perhaps we might make more headway by more frequently acknowledging that evolutionary hypotheses are actually quite difficult to test (as have Confer et al., 2010, for example), and that psychological studies are but one of many lines of converging evidence that are helping to put together the pieces of the puzzle. It is probably a fair criticism of our field that we rely too heavily on uncovering signs of special design of human psychological mechanisms as evidence of their evolution, and too little on examining the mechanism across species (Vonk and Shackelford, 2013). Other fields that are interested in the evolution of behavioral mechanisms routinely make phylogenetic comparisons, to test hypotheses. Even where we are proposing the evolution of a uniquely human adaptation, cross-species comparisons are (ultimately) necessary to test that idea. Of course not every paper needs to include such comparisons (particularly since they are often logistically difficult), but we may gain more widespread acceptance (or at least less widespread resistance) by explicitly acknowledging that without such comparisons many conclusions need to remain tentative.

I am not here arguing that we need cross species comparisons to test *whether* a mechanism evolved—I think we need to be working toward a broad psychology in which that is an unquestioned assumption—but to test *how* it evolved—using knowledge of phylogeny and ecological selective forces. To illustrate this, consider Burke and Sulikowski's (2010) demonstration that backward tilted faces (simulating viewing from below) are judged as more masculine (or less feminine) and forward tilted faces (simulating viewing from above) are judged to be more feminine (or less masculine). Based on this, they concluded that the structural sexual dimorphism in human faces, with males having larger jaws and smaller eyes, and females having smaller jaws and larger eyes, may have evolved to accentuate, or just make structural, the different appearance of faces viewed from above (as females tend to be seen by males) and below (as males tend to be seen by females), since males and females also differ in average height. The data are *consistent* with this conclusion, but it is strengthened by the fact that all of the hominins (who are all bipedal) show marked sexual height dimorphism, and the same face dimorphism as humans, but that the other apes (who are not bipedal) do not show the same face shape dimorphism. Of course this alone is not sufficient to conclude that the face shape differences *are* a consequence of an evolved signal exploiting the height-based perspective difference, but it is corroborating. Further evidence is required to rule out other possibilities, but the point of this example is to highlight that necessary and sufficient evidence won't always come from Psychology, or from humans.

The impression I get from my colleagues is that part of the indelibility of the stain of "just-so story telling" is related to the idea that EP is fundamentally focused on explaining (all) human behavior in terms of what would have been useful to our Hunter-Gatherer ancestors. Although it is true that we have spent the vast majority of our time as a species living such a lifestyle, it is almost certainly not true that most of our cognitive adaptations are *for* a "stone age" world—almost all of them very likely to predate this epoch considerably, and some may be newer. For example, almost every adaptation for perceiving the world (accounting for something like half of the neurons in the brain), was in place long before this epoch, and the mechanisms underpinning lactose tolerance, and resistance to particular localized diseases (e.g., malaria, plague) appear to have arisen later (Schaffner and Sabeti, 2008). Given that most EP is not actually about testing hypotheses specific to this epoch, since most studies tests hypotheses derived from fundamental evolutionary principles, one way of overcoming this misconception might be to try to more widely publicize those kinds of studies.

MOTIVATED OPPOSITION

Despite a noticeable (if gradual) shift away from what Tooby and Cosmides (1992) originally identified as the Standard Social Science Model, there remain pockets of vigorous opposition to the evolutionary approach to psychology. The main problem with this opposition is not the logic of the arguments or the strength of the evidence they provide against EP—typically they are weak, or based on a misunderstanding (Kurzban, 2010)—it is the fact that any kind of formal opposition provides a rationale for mainstream psychologists to keep ignoring evolutionary approaches.

There are clear signs that this opposition is motivated, rather than an inevitable consequence of a careful analysis of the accumulated evidence. Naturally, claims for which there is insufficient evidence are a concern in any field, and it is appropriate therefore to invite as much scrutiny as possible, but EP is the kind of field that has long had to deal with criticism (unfortunately much of it based on the next two factors discussed), and so is probably less likely than most fields to make claims for which there is insufficient evidence. One sign that some critiques are motivated is that they draw substantially broader conclusions than are warranted by their data and/or analyses. For example, Buller (2000, 2005) claims to have no issue with EP as a *field of enquiry* (generally taking an evolutionary approach to psychological questions) but is rather scathing of EP as a *paradigm* (by which he seems to mean the research done by the most prominent practitioners). Despite having no (avowed) problems with EP as a field of enquiry, he makes the very broad claim that there is *no* good evidence for *any* of the psychological adaptations that have been proposed. It is not unreasonable to suppose that critiques that find flaws with *all* of the claims that have been made might not be weighing up evidence in a completely unbiased way.

To further illustrate the nature of the problem, I will focus on a more recent critic of EP research, Christine Harris, who has published two failures to replicate evolutionarily inspired studies reporting shifts in women's judgments across the menstrual cycle. The first called into question the well-known (and indeed well-established) fluctuations in attractiveness judgments (Harris, 2011) and the most recent "failed to replicate" a shift in voting preferences (Harris and Mickes, 2014). Clear and cogent responses to both of these have been published, by the original researchers (DeBruine et al., 2010; Gildersleeve et al., 2013; Durante et al., 2014), identifying flaws in logic and methodology, but it is the broader conclusions Harris tries to draw that I believe reveal an obvious bias. Having failed to replicate one particular study of shifts in women's preferences for masculinized faces across the menstrual cycle (and having failed to review the large body of corroborating evidence), Harris (2011) concludes that we should be questioning "much of the current work in evolutionary psychology," especially those that identify "gender differences." This, of course, is not in any way warranted by the data, suggesting an obvious agenda. Similarly, despite a provocative (and politically charged) title—"Women can keep the vote: No evidence that hormonal changes during the menstrual cycle impact political and religious beliefs"—Harris and Mickes (2014) actually *did* replicate the interaction between menstrual cycle phase and relationship status on voting intentions—the most interesting aspect of the original study that they claim to have failed to replicate. Rather than attempting to get to the bottom of such an intriguing effect, their final conclusion is that their data add to a "growing number of failures to replicate several menstrual cycle effects on preferences" (they cite two), and essentially insinuate that the previous (very numerous) reports of positive effects of menstrual cycle phase on preferences are a consequence of "flexible" data analysis and fertility status classifications (for which there is no evidence).

It is difficult to be sure, but the tone of Harris' opposition to the evidence of menstrual cycle shifts in judgments suggests that it is based on the idea that such conclusions are somehow sexist—that they suggest that women's decisions are in some sense "at the mercy of their hormones." But I take the main message of this research to be that we are *all*, in some sense at least, at the mercy of our hormones (and not just gonadal ones), as they influence our decisions in evolutionarily adaptive ways. The preponderance of studies examining fluctuations across the menstrual cycle is almost certainly a simple consequence of the natural pseudo-experiment afforded by monthly variations in hormone balances. To look for the same effects in men, hormone levels need to be actually measured or manipulated, which makes such studies less common, but there is good evidence of strong effects of hormones on male behavior too (e.g., Mazur and Booth, 1998).

Of more concern than the opposition of any individual researcher (or group) is what quite obvious biases in published papers suggest about the broad attitudes of the field. It is worth wondering, for example, whether the "failed" replication of the Durante et al. (2013) paper would have ever been published in the absence of a broad (if potentially subtle) bias against evolutionary explanations (and/or those proposing sex differences based on something other than socialization differences) in mainstream psychology. Not only did the paper actually *not* fail to replicate the primary finding, it misrepresented the original authors' rationale (in a way that is consistent with well-known misunderstandings about evolutionary approaches being inherently sexist), was published despite at least one of the reviewers having sufficiently serious misgivings that they re-analyzed the data and found even more *consistencies* between the two studies, and was allowed to go to print with a title that clearly suggested that the original research *was* sexist, and with a conclusion that smears the entire body of literature examining shifts in preferences across the menstrual cycle. These are excesses that are typically not permitted. That they were permitted in a high-impact, mainstream psychology journal suggests the influence of a pervasive bias.

THEORETICAL INERTIA AND MISGUIDED SKEPTICISM

In general, in Science, skepticism is an invaluable tool, since it minimizes the risk of drawing conclusions on too little data, and especially of discarding existing theories without sufficient justification. But skepticism is frequently asymmetrical, with new approaches being more intensely scrutinized than old approaches. This is justified if the old approach is built on solid foundations, and has had much explanatory success, but there are good reasons for questioning whether this is true of many theories in psychology, especially since evolution was not one of the basic principles upon which they were built. I think that this asymmetrical skepticism might be at the heart of at least some of the bias against evolutionary approaches in mainstream psychology, even in the absence of any obviously motivated opposition.

The impression I have of the attitude of many of my colleagues is that there is no real *need* to adopt an evolutionary approach because psychology is doing fine without one, and this is associated with a reluctance to accept even *demonstrations* of the importance of an evolutionary perspective, with skeptics arguing that existing mechanisms (typically general process ones) are capable of explaining the results, and so there is just no need to propose "new" mechanisms. No doubt everyone who adopts an evolutionary approach in psychology has had to argue against these kinds of perspectives in their own sub-field, but in order to draw attention to the pervasiveness of the problem, I'd like to use an example of a general process mechanism that is accepted even by many evolutionarily oriented researchers (e.g., Shettleworth, 2010; Cosmides and Tooby, 2013)—the idea that there are general associative learning mechanisms.

The widespread acceptance of this view is an example of skepticism being directed only at new evidence, not at the evidence that underpins the traditional perspective. In fact, I think it is perfectly reasonable to claim not only that there is no good evidence that associative learning mechanisms are phylogenetically widespread (let alone evolutionarily conserved), but to question the very idea that *any* associative learning *mechanisms* have been established, at all. I understand that this claim seems extreme, but it is important to keep in mind that when we refer to classical (or Pavlovian) conditioning or to instrumental (or operant) conditioning, we are referring to learning *situations*—experimental paradigms that have been extensively used to study learning. What is actually learnt in these paradigms is very much a matter of ongoing debate (e.g., Gallistel, 1995; Gallistel and Gibbon, 2000), and it clearly depends on what is being learnt about, and which species is doing the learning (as famously demonstrated by Garcia and Koelling, 1966; Shettleworth, 1973; Timberlake, 2001). It is true that using a neutral stimulus to predict the arrival of a biologically (or at least behaviorally) significant stimulus (as in a Pavlovian conditioning experiment) leads to the production of anticipatory/preparatory behaviors in response to the previously neutral stimulus in a wide range of species, but this is no more evidence of a common *mechanism* in those species than the observation that a wide range of species can move from point A to point B is evidence of a common locomotion mechanism. The trouble here is that psychologists, as they rather too frequently do, have conflated a mechanism (*how* something works) with a functional category of behavior (what something *does*). There is actually no good evidence of universality of mechanism—indeed, an argument could be mounted that there is not a single species in which we understand *how* behavior is adjusted to exploit these simple environmental contingencies, short of the not especially helpful suggestion that the environmental association between the stimuli has somehow been "copied" inside the organism.

I have chosen this likely controversial example to try to illustrate that even ideas that seem so well established that they are essentially beyond question in psychology owe at least some of their power and influence to a long history of investigation, but that those factors are unrelated to the likelihood of the ideas being true. Given that almost all of the longest-established ideas in Psychology pre-date an evolutionary approach, we should expect a reluctance to accept the need to factor evolution in. Maybe the only way to overcome this resistance is to start using an evolutionary approach to dismantle some of those ideas, not by just suggesting that the standard social science model is an inappropriate one, given what we know about how mechanisms actually evolve, but by actively targeting particular (maybe especially popular) theories that cannot be easily accommodated within an evolutionary framework.

POOR UNDERSTANDING OF MODERN EVOLUTIONARY PRINCIPLES

I think the most fundamental problem in the more widespread acceptance of an evolutionary approach in psychology is the fact that very few psychology researchers or practitioners actually understand evolution, a problem that is considerably compounded by the fact that they are typically completely unaware of this. This is likely to be a consequence of the fact that most psychology degrees do not contain a good grounding in evolutionary theory. I teach at a well-rated university in a Psychology School that was one of only a handful in the country (Australia) to receive a 5 star ranking in the latest national quality assessment exercise, and I recently asked an advanced undergraduate class (in their 4th year) if they could describe the difference between natural and sexual selection. Only five (out of 113) of the students confidently knew the difference, despite evolutionary approaches being one of the topics (briefly) covered in the class. My students probably get exposed to more evolutionarily oriented psychology than most (certainly in Australia), but they do not, as is typical, do a class on evolution, and so they can't really be expected to have a proper appreciation of the insights such an understanding provides. An ability to even understand the importance of an evolutionary perspective in psychology depends, I think, on genuinely understanding how evolution works, and so we need to do what we can to pass on this *fundamental* knowledge if we hope to make evolution central in psychology. If our students (and I know this is also true of almost all of my colleagues) don't know the difference between sexual and natural selection, then they almost certainly don't know about Hamilton's rule and inclusive fitness, Trivers' Parental Investment Theory, condition-dependent strategies, honest signaling of mate quality, and a host of other concepts that are central to understanding the evolution of behavioral mechanisms in general. Given this, it is not surprising that they don't fully appreciate the power and importance of an evolutionary approach to psychology.

A clear illustration of this problem can be seen in many existing theories and debates in Psychology, perhaps most tellingly, even those purporting to be "evolutionary." For example, Ekman's (1992, 1997) well-known theory of universal emotion recognition and production is taken to be an evolutionary theory because there is cross-cultural consistency in the way in which the "basic" expressions are labeled. But the fundamental premise of the theory—that one's emotions erupt uncontrollably on the face, thus communicating them—is at odds with a modern understanding of the evolution of communicative signaling, in which the costs and benefits to the signaler and the receiver need to be weighed up, and in which a great deal of "communication" functions to "manipulate" other individuals (Krebs and Dawkins, 1984). A properly informed evolutionary perspective encourages us to ask how the expressions that we display increase our fitness, and how detecting and responding to them affects the fitness of the receivers.

Similarly, a great deal of debate in the face (identity) perception literature has focused on whether the Fusiform Face Area (FFA) only "processes" faces, or whether it is actually a part of the brain "for" perceiving any object that is habitually categorized at the subordinate level and with which we have substantial experience, and therefore expertise (e.g., Kanwisher et al., 1997; Gauthier et al., 1999). This debate has been widely construed as one between those who believe that there is an "evolved" "special" face area and those who hold that the apparent specialness is a consequence of expertise and the unusual nature of the stimuli being perceived. If the protagonists in this debate had a better grounding in the nature of evolved adaptations, they would not be using evidence that experience makes a difference to how some objects are "processed" to decide whether FFA is an evolved face perception area, since such effects are essentially orthogonal to whether the area originally evolved "*to*" perceive faces (Barrett, 2012; Burke and Sulikowski, 2013). Indeed, the fact that people can learn to use FFA to discriminate between "greebles" (artificial stimuli that differ in configural ways like faces) tells us as much about the evolved function of FFA as the fact that people can learn to ride bicycles tells us about the evolved function of legs.

WHAT TO DO?

To some extent EP is a victim of its own success. I think we all agree that stand-alone degree programs, and specialist conferences and journals are an important part of the field developing an identity and progressing without having to have protracted (and pointless) debates with those opposed to our approach, but they also have a tendency to isolate EP researchers (and maybe especially the new generation who are coming through the programs) from the core evolutionary biology and behavioral ecology that originally formed the inspiration for our discipline, and also from mainstream psychology. This isolation/protection has the potential to reduce the "selection pressure" on the field, and so to enable the proliferation of approaches that fall under the EP umbrella that are less rigorous than they would otherwise be. We would be wise to guard against this, to avoid providing opponents with genuine ammunition. Of course, it is almost inevitable that every area will produce some poor research, but given that EP faces motivated opposition in a way that most other sub-disciplines of psychology don't, and depends on a core of knowledge that most of our colleagues don't have, we need to be especially careful to ensure that our output is as rigorous and well-informed as it can possibly be. It might also be helpful to be conscious of the nature of the opposition our findings may face, and the ways in which they may be misunderstood, and to preemptively allay them in our published papers, and especially in our dealings with the media (when this is possible).

In addition to courses on EP itself (ideally with comparative psychology integrated into them), I think it is important that all psychology students learn basic evolutionary biology and behavioral ecology (and maybe physical anthropology where such classes still exist)—completely independently of psychology. This comprises much of the core knowledge they need to approach psychology from an evolutionary perspective, both in terms of the actual content of such classes, but also in the mere fact of being exposed to complex adapted mechanisms in a wide range of species, giving them the appropriate perspective on human behavioral mechanisms. I suspect that without producing a generation of psychology students who properly understand evolution, we will always be fighting a losing battle to have evolutionary approaches integrated into mainstream psychology. Even if we could, overnight, instill a burning *desire* in all psychologists to approach their research from an evolutionary perspective, this would likely hinder more than help our field because they would be *unable* to do research that is properly informed by an understanding of evolution.

Although I think it is important to publish our *findings* in mainstream psychology journals (arduous though this task can be), I think it might actually be a good idea to *stop* trying to explain what EP *is* to those outside the field. So far that seems to have served mostly to focus opposition, and as I have argued here, some of that opposition might be at least partially justified. As a brief survey of the kinds of papers being published in the field shows, the summaries that have been produced don't really reflect the majority of the research being conducted, anyway. I wonder if a more effective strategy might be to instead target mainstream (ideally high impact) outlets for findings that either would never have been investigated without an evolutionary approach, or of phenomena that make no sense except in light of evolution. EP is also a very media-friendly discipline (something that I suspect makes us more of a target from our mainstream colleagues than we might otherwise be). Ideally, we would be able to use that interest in a more strategic way than we currently do, again, by making more widely known studies in which aspects of human psychology only make sense in light of well-established, general evolutionary principles—the kinds of findings that don't depend on any untested assumptions about our recent ancestors, or the structure and nature of our cognitive mechanisms, but rather are straightforward, essentially irrefutable corollaries of fundamental evolutionary principles. A good example of such a finding is the MHC-dependent odor preferences discovered by Wedekind et al. (1995). These are the kinds of findings that I believe are most likely to convince skeptics of the value of our approach, and which could lay the foundations of a psychology that genuinely integrates evolution.

REFERENCES

Barkow, J. H., Cosmides, L., and Tooby, J. (eds.). (1992). *The Adapted Mind: Evolutionary Psychology and the Generation of Culture.* New York, NY: OUP.

Barrett, H. C. (2012). A hierarchical model of the evolution of human brain specializations. *Proc. Natl. Acad. Sci. U.S.A.* 109, 10733–10740. doi: 10.1073/pnas.1201898109

Barrett, H. C., and Kurzban, R. (2006). Modularity in cognition: framing the debate. *Psychol. Rev.* 113, 628–647. doi: 10.1037/0033-295X.113.3.628

Barrett, L., Pollet, T., and Stulp, G. (2014). From computers to cultivation: reconceptualizing evolutionary psychology. *Front. Psychol.* 5:867. doi: 10.3389/fpsyg.2014.00867

Buller, D. J. (2000). "A guided tour of evolutionary psychology," in *A Field Guide to the Philosophy of Mind*, eds M. Nani and M. Marraffa (An Official Electronic Publication of the Department of Philosophy of University of Rome 3).

Buller D. J. (2005). Evolutionary psychology: the emperor's new paradigm. *Trends Cogn. Sci.* 9, 277–283. doi: 10.1016/j.tics.2005.04.003

Burke, D., and Fulham, B. J. (2003). An evolved spatial memory bias in a nectar-feeding bird? *Anim. Behav.* 66, 695–701. doi: 10.1006/anbe.2003.2246

Burke, D., and Sulikowski, D. (2010). A new viewpoint on the evolution of sexually dimorphic human faces. *Evol. Psychol.* 8, 573–585.

Burke, D., and Sulikowski, D. (2013). The evolution of holistic processing of faces. *Front. Psychol.* 4:11. doi: 10.3389/fpsyg.2013.00011

Buss, D. M. (ed.). (2005). *The Handbook of Evolutionary Psychology*. Hoboken, NJ: Wiley.

Buss, D. M., Haselton, M. G., Shackelford, T. K., Bleske, A. L., and Wakefield, J. C. (1998). Adaptations, exaptations, and spandrels. *Am. Psychol.* 53, 533–548. doi: 10.1037/0003-066X.53.5.533

Confer, J. C., Easton, J. A., Fleischman, D. S., Goetz, C. D., Lewis, D. M. G., Perilloux, C., et al. (2010). Evolutionary psychology: controversies, questions, prospects, and limitations. *Am. Psychol.* 65, 110–126. doi: 10.1037/a0018413

Cosmides, L., and Tooby, J. (2013). Evolutionary psychology: new perspectives on cognition and motivation. *Annu. Rev. Psychol.* 64, 201–229. doi: 10.1146/annurev.psych.121208.131628

DeBruine, L., Jones, B. C., Frederick, D. A., Haselton, M. G., Penton-Voak, I. S., and Perrett, D. I. (2010). Evidence for menstrual cycle shifts in women's preferences for masculinity: a response to Harris (in press) "Menstrual cycle and facial preferences reconsidered." *Evol. Psychol.* 8, 768–775.

Durante, K. M., Rae, A., and Griskevicius, V. (2013). The fluctuating female vote: politics, religion, and the ovulatory cycle. *Psychol. Sci.* 24, 1007–1016. doi: 10.1177/0956797612466416

Durante, K. M., Rae, A., and Griskevicius, V. (2014). Fertility can have different effects on single and nonsingle women: reply to Harris and Mickes (2014). *Psychol. Sci.* 25, 1150–1152. doi: 10.1177/0956797614524422

Ekman, P. (1992). Are there basic emotions? *Psychol. Rev.* 99, 550–553. doi: 10.1037/0033-295X.99.3.550

Ekman, P. (1997). Should we call it expression or communication? *Innov. Soc. Sci. Res.* 10, 333–344. doi: 10.1080/13511610.1997.9968538

Gaffan, E. A., and Davies, J. (1981). The role of exploration in win-shift and win-stay performance on a radial maze. *Learn. Motiv.* 12, 282–299. doi: 10.1016/0023-9690(81)90010-2

Gaffan, E. A., and Davies, J. (1982). Reward, novelty and spontaneous alternation. *Q. J. Exp. Psychol.* 34B, 31–47.

Gallistel, C. R. (1995). "The replacement of general purpose theories with adaptive specializations," in *The Cognitive Neurosciences*, ed M. S. Gazzaniga (Cambridge, MA: MIT Press), 1255–1267.

Gallistel, C. R., and Gibbon, J. (2000). Time, rate, and conditioning. *Psychol. Rev.* 107, 289–344. doi: 10.1037/0033-295X.107.2.289

Garcia, J., and Koelling, R. A. (1966). Relation of cue to consequence in avoidance learning. *Psychon. Sci.* 4, 123–124. doi: 10.3758/BF03342209

Gauthier, I., Tarr, M., Anderson, A., Skudlarski, P., and Gore, J. (1999). Activation of the middle fusiform 'face area' increases with expertise in recognising novel objects. *Nat. Neurosci.* 2, 568–573. doi: 10.1038/9224

Gibson, J. J. (1979). *The Ecological Approach to Visual Perception*. Boston, MA: Houghton Mifflin.

Gildersleeve, K., DeBruine, L., Haselton, M. G., Frederick, D. A., Penton-Voak, I. S., Jones, B. C., et al. (2013). Shifts in women's mate preferences across the ovulatory cycle: a critique of Harris (2011) and Harris (2012). *Sex Roles* 69, 516–524. doi: 10.1007/s11199-013-0273-4

Harris, C. R. (2011). Menstrual cycle and facial preferences reconsidered. *Sex Roles* 64, 669–681. doi: 10.1007/s11199-010-9772-8

Harris, C. R., and Mickes, L. (2014). Women can keep the vote: no evidence that hormonal changes during the menstrual cycle impact political and religious beliefs. *Psychol. Sci.* 25, 1147–1149. doi: 10.1177/0956797613520236

Kamil, A. C. (1978). Systematic foraging by a nectar-feeding bird, the Amakihi (Loxops virens). *J. Comp. Physiol. Psychol.* 92, 388–396. doi: 10.1037/h0077479

Kamil, A. C. (1988). "A synthetic approach to the study of animal intelligence," in *Nebraska Symposium on Motivation*, Vol. 35, ed D. W. Leger (Lincoln, MA: University of Nebraska Press), 257–308.

Kanwisher, N., McDermott, J., and Chun, M. (1997). The fusiform face area: a module in human extrastriate cortex specialised for face perception. *J. Neurosci.* 17, 4302–4311.

Krebs, J. R., and Dawkins, R. (1984). "Animal signals: mind-reading and manipulation," in *Behavioural Ecology*, eds J. R. Krebs and N. B. Davies (Oxford: Blackwell), 380–402.

Kurzban, R. (2010). Grand challenges of evolutionary psychology. *Front. Psychol.* 1:3. doi: 10.3389/fpsyg.2010.00003

Mazur, A., and Booth, A. (1998). Testosterone and dominance in men. *Behav. Brain Sci.* 21, 353–397. doi: 10.1017/S0140525X98001228

McNamara, J. M., and Houston, A. I. (2009). Integrating function and mechanism. *Trends Ecol. Evol.* 24, 670–675. doi: 10.1016/j.tree.2009.05.011

Schaffner, S., and Sabeti, P. (2008). Evolutionary adaptation in the human lineage. *Nat. Educ.* 1, 14.

Shettleworth, S. J. (1973). "Food reinforcement and the organization of behaviour in golden hamsters," in *Constraints on Learning: Limitations and Predispositions*, eds R. A. Hinde and J. S. Hinde (New York, NY: Academic Press), 243–263.

Shettleworth, S. J. (2010). *Cognition, Evolution, and Behavior*. Oxford: OUP.

Stotz, K. (2014). Extended evolutionary psychology: the importance of transgenerational developmental plasticity. *Front. Psychol.* 5:908. doi: 10.3389/fpsyg.2014.00908

Sulikowski, D., and Burke, D. (2007). Food-specific spatial memory biases in an omnivorous bird. *Biol. Lett.* 3, 245–248. doi: 10.1098/rsbl.2007.0122

Sulikowski, D., and Burke, D. (2010a). Reward type influences performance and search structure of an omnivorous bird in an open-field maze. *Behav. Process.* 83, 31–35. doi: 10.1016/j.beproc.2009.09.002

Sulikowski, D., and Burke, D. (2010b). When a place is not a place: encoding of spatial information is dependent on reward type. *Behaviour* 147, 1461–1479. doi: 10.1163/000579510X521564

Sulikowski, D., and Burke, D. (2011). Movement and memory: different cognitive strategies are used to search for resources with different natural distributions. *Behav. Ecol. Sociobiol.* 65, 621–631. doi: 10.1007/s00265-010-1063-4

Sulikowski, D., and Burke, D. (2012). Win-shifting in nectarivorous birds: selective inhibition of the learned win-stay response. *Anim. Behav.* 83, 519–524. doi: 10.1016/j.anbehav.2011.11.030

Timberlake, W. (2001). Integrating niche-related and general process approaches in the study of learning. *Behav. Process.* 54, 79–94. doi: 10.1016/S0376-6357(01)00151-6

Tooby, J., and Cosmides, L. (1992). "The psychological foundations of culture," in *The adapted mind: Evolutionary Psychology and the Generation of Culture*, eds J.

Barkow, L. Cosmides, and J. Tooby (New York, NY: Oxford University Press), 19–136.

Vonk, J., and Shackelford, T. K. (2013). An introduction to comparative evolutionary psychology. *Evol. Psychol.* 11, 459–469.

Wedekind, C., Seebeck, T., Bettens, F., and Paepke, A. J. (1995). MHC-dependent mate preferences in humans. *Proc. Biol. Sci.* 260, 245–249. doi: 10.1098/rspb.1995.0087

Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 09 June 2014; accepted: 30 July 2014; published online: 27 August 2014.
Citation: Burke D (2014) Why isn't everyone an evolutionary psychologist? Front. Psychol. ***5****:910. doi: 10.3389/fpsyg.2014.00910*
This article was submitted to Evolutionary Psychology and Neuroscience, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

OPINION ARTICLE
published: 10 October 2014
doi: 10.3389/fpsyg.2014.01158

Putting the theory before the data: is "massive modularity" a necessary foundation of evolutionary psychology?

Ian D. Stephen*

Department of Psychology and Evolutionary Psychology Research Group, Macquarie University, Sydney, NSW, Australia
**Correspondence: ian.stephen@mq.edu.au*

Edited by:
Danielle Sulikowski, Charles Sturt University, Australia

Reviewed by:
Thomas Pollet, VU University Amsterdam, Netherlands

Keywords: massive modularity, evolutionary psychology, EEA, Santa Barbara school, human ethology

In this volume, Burke (2014) makes a number of arguments for why evolutionary approaches have failed to penetrate the rest of the field of psychology (what Burke refers to as "mainstream" psychology). While all of his arguments have merit, I will focus on one that I consider to be particularly important—the characterization by critics of the "Santa Barbara school" (Laland and Brown, 2011) as representative of all evolutionary approaches to psychology. Here, I agree with this point, and I expand upon Burke's point to argue that the focus on massive modularity as one of the foundational principles of evolutionary psychology is "putting the theory before the data," and opens the discipline to criticism that is unwarranted for many of its researchers.

In 2013, I was fortunate to attend a talk by John Richer at the International Society for Human Ethology's Summer Institute, who argued that there is much to be gained from applying the ethological methodology of observation and documentation to clinical psychology settings. He was advocating deviating from hypothesis and experimentation, and applying a technique more akin to the production of ethnographies in social anthropology (Richer, 2014). While initially resistant to the idea, I later read Rozin's (2001) critique of the state of social psychological research. A comparison is made to Darwin's theory of evolution by natural selection which, he argues, was the result of a large body of observation, description and documentation that took place before the formalization of foundational principles. It grew out of an empiricist—as opposed to theorist—desire to understand the origins of species. Rozin argues that social psychology, in its rush to model itself on more established lines of research, such as biology and cognitive science, has skipped these important stages of observation and description, which he considers so critical to the development of a young discipline. In so doing, Rozin argues, social psychologists have rushed to formalize as theoretical underpinnings of the discipline ideas that have little supporting evidence, and have greatly restricted the range of acceptable topics for investigation within the field.

The situation in evolutionary psychology is similar, though not identical. Early in its conception, researchers attempted to formalize the field with a set of foundational principles—typically evolved psychological mechanisms, massive modularity of mind/domain specificity and the concept of an environment of evolutionary adaptedness, often assumed to be the Pleistocene (Cosmides and Tooby, 1987). These principles are not universally accepted within the community of researchers who take an evolutionary approach to psychology (Laland and Brown, 2011), and Burke (2014) argues that the massively modular view of the brain is not necessary for the application of evolutionary theory to psychology. Indeed, most research in the field is focused on gathering observations and testing hypotheses derived from fundamental evolutionary principles, rather than from the Santa Barbara school's formulation (Burke, 2014).

In most discussions about modularity and plasticity in the mind, the argument is really over the degree of modularity in the mind, and therefore the level on which selection operates. In much of the research being conducted in the field of evolutionary approaches to psychology, this distinction is, however, largely irrelevant. In contrast to the criticisms of many critics of evolutionary approaches to behavior (Benton, 2000), even adherents to the Santa Barbara school's formulation predict the evolution of flexible mental modules in order to allow flexibility of behavior in response to environmental and internal factors (Kurzban, 2002; see also Sperber, 2005). Consider the example of men's preferences for women's body size, which is hypothesized to represent a preference for healthy weight given the local environmental conditions. Men living in areas of food scarcity prefer higher BMI women, as this is most adaptive, while men in areas of food security prefer lower BMI women, as this is most adaptive given the local conditions (Tovée et al., 2006). This same hypothesis follows equally from a massive modularity, Santa Barbara school approach as from a mental plasticity, cultural evolution approach. The Santa Barbara school approach predicts that an evolved mental module for body size preference should have been selected to be sensitive to local ecological conditions, and would therefore predict the pattern of higher BMI preferences in areas of food scarcity and lower BMI preferences in areas of food security. A more moderate modularity approach would predict a mental module for attractiveness that can learn the appropriate preferences given the local ecological conditions, and thus predict the same pattern. Finally, a mental plasticity, cultural evolution approach would predict that culturally transmitted body size preferences would result in fitness benefits for those who carried the appropriate body size preference given the local ecological conditions, and would therefore predict the same pattern. It is not necessary to commit to one of these models of mind in order to formulate hypotheses based on evolutionary predictions (Burke, 2014). The necessary foundational principles are merely that behavior, cognition and perception have fitness consequences, and that selection shapes behavior, perception and cognition; something upon which all researchers adopting evolutionary approaches to psychology can surely agree.

While mainstream cognitive psychology and neuroscience are producing some convincing data that different types of information are processed in different brain regions—which could be considered modules—and there have been some well-reasoned defenses of the concept of massive modularity (e.g., Barrett and Kurzban, 2006), the conception of the massively modular mind lacks sufficient empirical evidence (Laland and Brown, 2011). Burke (2014) points out that, in the absence of alternative formally articulated sets of foundational principles, the Santa Barbara school's formulation presents critics of evolutionary approaches to psychology with a supposed foundational principle that lacks a solid empirical basis, and allows these critics to dismiss the entire field as built on shaky foundations. Ironically, the criticism that is aimed at evolutionary approaches to psychology (which, it should be noted, began well before the formalization of the Santa Barbara principles) provides substantial pressure to formalize that other disciplines did not have to weather during their early stages (Rozin, 2001). Laland and Brown (2011) point out that Wilson felt that sociobiology was held up to unfair standards: "While the sociological or cultural model is assumed to be true unless proven false beyond any possible doubt, the biological model is assumed to be false unless evidence is completely unassailable in their support." This could also be said of evolutionary approaches to psychology more generally.

So where to from here? Others in this volume argue that the massive modularity of mind is an empirical question (Barrett et al., 2014), and I strongly agree. It may well turn out to be true, but before identifying this model of mind as a foundational principle, it is important to ensure that it is well supported empirically. In the meantime, it is encouraging to note that the early attempt to formalize foundational principles has not led to the over-focus on a small number of topics and techniques that Rozin (2001) decries in social psychology. Evolutionary approaches to psychology investigate a wide range of topics, from mate selection, life history strategy, food gathering and sharing, cooperation and altruism, aggression, gender roles, and parenting, and use a wide range of techniques—experimental psychological techniques, game theory, ethology, and ethnographic observations to name but a few. Anyone who attends HBES, EHBEA, ISHE or any of the other conferences dedicated to the approach will discover that new fields of study are constantly being approached through the lens of evolutionary theory.

In conclusion, then, while there is pressure from critics of the field to declare a set of foundational principles for the field, including determining whether or not the mind is domain specific and massively modular, these are empirical questions that require further research. Further, the structure of the mind is not a prerequisite for the investigation of psychology through an evolutionary lens. The field should therefore continue to research the question of modularity of mind, and continue to explore the broad range of human behavior and cognition through observation, documentation and hypothesis generation and testing. There is little to be gained by prematurely formalizing the foundations of the field—putting the theory before the data—particularly if those foundations later turn out to be shaky.

ACKNOWLEDGMENT

I would like to thank Prof Dick Stevenson for his discussion about the topic.

REFERENCES

Barrett, H. C., and Kurzban, R. (2006). Modularity in cognition: framing the debate. *Psychol. Rev.* 113, 628–647. doi: 10.1037/0033-295XX.113.3.628

Barrett, L., Pollet, T., and Stulp, G. (2014). From computers to cultivation: reconceptualising evolutionary psychology. *Front. Psychol.* 5:867. doi: 10.3389/fpsyg.2014.00867

Benton, T. (2000). "Social causes and natural relations," in *Alas Poor Darwin: Arguments Against Evolutionary Psychology,* eds H. Rose and S. Rose (New York, NY: Harmony Books), 249–270.

Burke, D. (2014). Why isn't everyone an evolutionary psychologist? *Front. Psychol.* 5:910. doi: 10.3389/fpsyg.2014.00910

Cosmides, L., and Tooby, J. (1987). "From evolution to behaviour: evolutionary psychology as the missing link," in *The Latest on the Best: Essays on Evolution and Optimality,* ed J. Dupre (Cambridge, MA: The MIT Press), 277–306.

Kurzban, R. (2002). Alas poor evolutionary psychology: unfairly accused, unjustly condemned. *Hum. Nat. Rev.* 2, 99–109. Available online at: http://human-nature.com/nibbs/02/apd.html

Laland, K., and Brown, G. (2011). *Sense and Nonsense: Evolutionary Perspectives on Human Behaviour, 2nd Edn.* Oxford: Oxford University Press.

Richer, J. (2014). "Disordered" behaviour. Alternatives to DSM-5 from and ethological perspective. *Hum. Ethol. Bull.* 29, 27–55. Available online at: http://media.anthro.univie.ac.at/ishe_journal/index.php/heb/article/view/113/100

Rozin, P. (2001). Social psychology and science: Some lessons from Solomon Asch. *Pers. Soc. Psychol. Rev.* 5, 2–14. doi: 10.1207/S15327957PSPR0501_1

Sperber, D. (2005). "Dan Sperber. 2005. Modularity and relevance: how can a massively modular mind be flexible and context-sensitive?," in *The Innate Mind: Structure and Content,* eds P. Carruthers, S. Laurence, and Stich, S (Oxford: Oxford University Press), 53–68.

Tovée, M. J., Swami, V., Furnham, A., and Mangalparsad, R. (2006). Changing perceptions of attractiveness as observers are exposed to a different culture. *Evol. Hum. Behav.* 27, 443–456. doi: 10.1016/j.evolhumbehav.2006.05.004

Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 25 August 2014; accepted: 24 September 2014; published online: 10 October 2014.

Citation: Stephen ID (2014) Putting the theory before the data: is "massive modularity" a necessary foundation of evolutionary psychology? Front. Psychol. ***5****:1158. doi: 10.3389/fpsyg.2014.01158*

This article was submitted to Evolutionary Psychology and Neuroscience, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

OPINION ARTICLE
published: 11 November 2014
doi: 10.3389/fpsyg.2014.01212

How beliefs get in the way of the acceptance of evolutionary psychology

Peter K. Jonason[1]* **and Laura K. Dane**[2]

[1] School of Social Sciences and Psychology, University of Western Sydney, Milperra, NSW, Australia
[2] Psychology, Douglas College, New Westminster, BC, Canada
*Correspondence: peterkarljonason@yahoo.com

Edited by:
Danielle Sulikowski, Charles Sturt University, Australia

Reviewed by:
Joanne Souza, Stony Brook University, USA

Keywords: evolutionary psychology, biases, belief systems, social psychology, philosophy

There can be no doubt there is serious resistance to evolutionary psychology (EP) as a theoretical paradigm from both within the field (e.g., social psychology) and in other disciplines (e.g., social sciences). Numerous researchers (Harris, 2003; Eastwick et al., 2014) appear to have made it their objective to show how predictions made and studies conducted by evolutionary psychologists are flawed (and even outright sexist). Such research programs have left evolutionary psychologists scratching their heads with the simple, yet fundamental question of why is everyone not an evolutionary psychologist?

Darren Burke (DB) details institutional biases in promoting evolutionary sciences. In the United States this shows itself in the debate about teaching Creationism or Intelligent Design in schools as an apparently reasonable effort to be balanced. Ironically, evolved mechanisms for extended collaborative actions with kin and non-kin to exploit resources may be responsible for financial, political, and intellectual collusions to maintain the very belief systems that spawned them. These may create institutional blocks in terms of funding, publishing, and hiring practices. As academics trained in psychology as well as biology and anthropology, we focus on individual-level obstacles to complement DB's position. We focus on the potential psychological reasons behind the resistance to EP.

We contend there are essentially four different types of psychological resistance to EP, all of which are a function of an individual's philosophical belief systems, whether they are implicit or explicit. The biases are not unique to mainstream psychology or even researchers but, instead, may be endemic in people, more generally. We focus our attention on researchers because we wish to draw attention to biases in those who have been educated to be less biased. This is not to say we are not biased in our own way. We, like most evolutionary psychologists, assume human beings are part of the natural world; the only explanations worth attending to are naturalistic; and the brain (and all that comes from it) is a naturally occurring, evolved aspect of humans. Assumptions pervade all of science, what matters is holding the fewest and most reasonable assumptions possible. We feel the theory of evolution offers just that, but there may be a series of psychological blocks that exclude individuals from thinking clearly about evolution in reference to humans and to eschew what evolutionary predictions/findings mean.

RELIGIOUS THINKING

The first, most obvious objection stems from the denial of evolution *en toto*. Such beliefs normally stem from religious beliefs about the nature of the universe, human's place it in, and the active effort to maintain those beliefs. Many liberal and famous academics (e.g., Stephen Jay Gould) walk the line between belief in the supernatural/metaphysical and science by arguing that science and religion deal with "non-overlapping magisteria" (Gould, 1998, p. 274). This political view is functional for many scientists who, for want of protecting their own beliefs (often implicitly), protecting their own reputation, ensuring they do not lose their jobs, and securing funding from government agencies who are likely staffed by people who fundamentally disagree with all things related to evolution, may steer away from such topics or paradigms. However, psychological science (in particular) does overlap with questions of moral value and reasoning, and some religious claims overlap with scientific empiricism. Objections to the evolutionary study of human behavior, from this perspective, are hard to overcome because the motivation behind the denial stems from a (perceived) need to protect one's values and morals. If science is a pursuit of empirical evidence to support or falsify predictions derived from theory there can be no doubt that naturalistic predictions, derived from evolutionary theory are not only sound but must have relevance to human beings.

HUMAN EXCEPTIONALISM

The second philosophical objection centers around a Spencerian version of the Darwin-Wallace theory of evolution. Many psychological and social scientists accept the theory of evolution in principle but deny that it is relevant to studying human cognition or behavior (i.e., Cartesian Dualism). Many can accept that our bipedal gate, relative hairlessness, or cranial structures have evolved through natural/sexual selection, but an application of the same principles to human behavior receives a vehement rejection. This position has implicitly haunted psychology for decades and we can see it today in the constant attempts to define what makes humans special relative to other animals (e.g., language; Pinker, 1994; culture; Henrich and McElreath, 2003; play; Maestripieri, 2012) and the implicit belief that the human brain needs its own science that is separate from biology. While these objections do not necessarily come from a religious background, there is an underlying sense that a naturalistic approach to human behavior threatens existing views of morals or ethics (see Curry, 2006).

ENVIRONMENTAL DETERMINISM

The third philosophical objection comes from those who may allow biology some role in explaining human behavior but the role is extremely limited. The obvious one of relevance comes in many names: The Standard Social Sciences Model, Tabula Rasa, and Environmental Determinism. All of these hold at their core the personal, political, or professional "need" to believe that human beings are more a product of environmental influences than evolved differences (see Genetic Determinism below). This ideology was most strongly expressed in behaviorism but still is predominant in social psychology textbooks and conferences. For instance, Worchel and Cooper (1976) say that "social psychology is the study of the way in which individuals are affected by social situations" (p. 7) and Shaver (1977) says social psychology is "the scientific study of the personal and situational factors that affect individual social behavior" (p. 14). This bias in focusing on the environmental, social, or cultural causes of human behavior is functional in that it allows researchers to suggest ways we can change behavior. This position is not all bad, except it leads to a pure focus on proximate mechanisms. This is not to say that all behaviors have ultimate, evolutionary causes, but an understanding of the potential ultimate functions of various aspects of human nature can lead to an even better understanding of how to change behavior. Nevertheless, in both cases researchers need to be more critical about understanding their topic of interest in macroscopic and microscopic levels (Bingham and Souza, 2009).

GENETIC DETERMINISM

Not only is there a gross misunderstanding of the theory of evolution (and its application to human behavior), but also there seems to be an active bias against learning about genetics and comparative biology. These "inferential prisons" leave researchers hard-pressed to explain many observed effects (e.g., twin concordance in personality; Vernon et al., 2008) and they are at a disadvantage compared to evolutionary psychologists whose models are expressly about the interaction of the person and the environment. EP and related disciplines like evolutionary developmental psychology (Evo Devo) ARE environmentalist disciplines. Take as an example the research on kin recognition and incest avoidance (Lieberman et al., 2007). The authors propose an innate learning process which, helps us determine who our siblings are (and therefore who to help and who not to mate with) through the length of sibling co-residence and the other child's perinatal association with one's mother. The degree to which these "environmental" factors are present depends on whether the individual is an older or younger sibling. A second born will of course not be exposed to cues of her sibling's perinatal association with their mother but will have cues to co-residence if she is raised with her sibling. This research is consistent with the Westermark hypothesis (1981), which fell out of favor in the 20th century partially because the SSSM belief that behavior is predominately environmentally determined. But if an evolutionary approach is consistent with environmental determinants of human behavior then why do many psychologists have issues with the discipline? The difference is that many social psychologists hold an implicit belief in a version of tabula rasa, or general purpose learning in humans (Lieberman and Symons, 1998). The Westermark hypothesis, like discussion of kin recognition mechanisms, leads many to think of genetically determined, automatic systems that tell us exactly who we are related to. This could not be farther from what the comparative biologists and evolutionary psychologists are arguing. Our brains estimate relatedness based on cues (environmental contingencies) that must be experienced through development (learning). The end result is not perfect knowledge of who we are related to, but best guesses based on available information that, on average over time, would have lead us to make decisions that increased inclusive fitness. We would argue that these specific cues and their specific effects on sibling altruism and incest aversion could only have been predicted from a perspective taking the evolved function of kin recognition into account.

DB argues for increased training in evolutionary theory, which logically should temper many of the objections to evolutionary approaches to psychology. However, we suggest that attention should be paid to the underlying motivations behind the critiques from social scientists. As long as EP is perceived to threaten political (e.g., men and women should be equal), moral (e.g., humans should be inherently nice), professional (e.g., all behavior is changeable), and religious (e.g., God created us in our present, immutable form) belief systems, the cognitive biases underlying those systems will act to preserve them. We fear that without the anchor that is Evolutionary Theory (see Confer et al., 2010), psychology as a science will continue to pitch and yaw through the sea.

REFERENCES

Bingham, P. M., and Souza, J. (2009). *Death From a Distance and the Birth of a Humane Universe.* Lexington, KY: BookSurge Publishing.

Confer, J. C., Easton, J. A., Fleischman, D. S., Goetz, C. D., Lewis, D. M. G., Perilloux, C., et al. (2010). Evolutionary psychology: questions, prospects, and limitations. *Am. Psychol.* 65, 110–126. doi: 10.1037/a0018413

Curry, O. (2006). Who's afraid of the naturalistic fallacy? *Evol. Psychol.* 4, 234–247.

Eastwick, P. W., Luchies, L. B., Finkel, E. J., and Hunt, L. L. (2014). The predictive validity of ideal partner preferences: a review and meta-analysis. *Psychol. Bull.* 140, 623–681. doi: 10.1037/a0032432

Gould, S. J. (1998). *Leonardo's Mountain of Clams and the Diet of Worms.* Boston, MA: Jonathan Cape. doi: 10.4159/harvard.9780674063365

Harris, C. R. (2003). A review of sex differences in sexual jealousy, including self-report data, psychophysiological responses, interpersonal violence, and morbid jealousy. *Pers. Soc. Psychol. Rev.* 7, 102–128. doi: 10.1207/S15327957PSPR0702_102-128

Henrich, J., and McElreath, R. (2003). The evolution of cultural evolution. *Evol. Anthropol.* 12, 123–135. doi: 10.1002/evan.10110

Lieberman, D., and Symons, D. (1998). Sibling incest avoidance: from westermark to wolf. *Q. Rev. Biol.* 73, 463–466. doi: 10.1086/420414

Lieberman, D., Tooby, J., and Cosmides, L. (2007). The architecture of human kin detection. *Nature* 15, 727–731. doi: 10.1038/nature05510

Maestripieri, D. (2012). *Games Primates Play.* New York, NY: Basic Books.

Pinker, S. (1994). *The Language Instinct*. New York, NY: Penguin Books.

Shaver, K. G. (1977). *Principles of Social Psychology*. Cambridge, MA: Winthrop.

Vernon, P. A., Villani, V. C., Vickers, L. C., and Harris, J. A. (2008). A behavioral genetics investigation of the Dark Triad and the Big 5. *Pers. Individ. Dif.* 44, 445–452. doi: 10.1016/j.paid.2007.09.007

Westermark, E. (1981). *History of Human Marriage*. London: Macmillan and Co.

Worchel, S., and Cooper, J. (1976). *Understanding Social Psychology.* Homewood, IL: Dorsey Press.

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 21 August 2014; accepted: 06 October 2014; published online: 11 November 2014.

Citation: Jonason PK and Dane LK (2014) How beliefs get in the way of the acceptance of evolutionary psychology. Front. Psychol. ***5****:1212. doi: 10.3389/fpsyg.2014.01212*

This article was submitted to Evolutionary Psychology and Neuroscience, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

REVIEW ARTICLE
published: 12 August 2014
doi: 10.3389/fpsyg.2014.00867

From computers to cultivation: reconceptualizing evolutionary psychology

Louise Barrett[1]*, Thomas V. Pollet[2] and Gert Stulp[3]

[1] Department of Psychology, University of Lethbridge, Lethbridge, AB, Canada
[2] Department of Social and Organizational Psychology, VU University Amsterdam, Amsterdam, Netherlands
[3] Department of Population Health, London School of Hygiene and Tropical Medicine, London, UK

Edited by:
Danielle Sulikowski, Charles Sturt University, Australia

Reviewed by:
Ben Colagiuri, University of New South Wales, Australia
Karola Stotz, Macquarie University, Australia

***Correspondence:**
Louise Barrett, Department of Psychology, University of Lethbridge, 4401 University Drive West, Lethbridge, AB T1K 3M4, Canada
e-mail: louise.barrett@uleth.ca

Does evolutionary theorizing have a role in psychology? This is a more contentious issue than one might imagine, given that, as evolved creatures, the answer must surely be yes. The contested nature of evolutionary psychology lies not in our status as evolved beings, but in the extent to which evolutionary ideas add value to studies of human behavior, and the rigor with which these ideas are tested. This, in turn, is linked to the framework in which particular evolutionary ideas are situated. While the framing of the current research topic places the brain-as-computer metaphor in opposition to evolutionary psychology, the most prominent school of thought in this field (born out of cognitive psychology, and often known as the Santa Barbara school) is entirely wedded to the computational theory of mind as an explanatory framework. Its unique aspect is to argue that the mind consists of a large number of functionally specialized (i.e., domain-specific) computational mechanisms, or modules (the massive modularity hypothesis). Far from offering an alternative to, or an improvement on, the current perspective, we argue that evolutionary psychology is a mainstream computational theory, and that its arguments for domain-specificity often rest on shaky premises. We then go on to suggest that the various forms of e-cognition (i.e., embodied, embedded, enactive) represent a true alternative to standard computational approaches, with an emphasis on "cognitive integration" or the "extended mind hypothesis" in particular. We feel this offers the most promise for human psychology because it incorporates the social and historical processes that are crucial to human "mind-making" within an evolutionarily informed framework. In addition to linking to other research areas in psychology, this approach is more likely to form productive links to other disciplines within the social sciences, not least by encouraging a healthy pluralism in approach.

Keywords: evolutionary psychology, cognition, cognitive integration, modules, extended mind

INTRODUCTION

As evolved beings, it is reasonable to assume that evolutionary theory has something to offer the study of human psychology, and the social sciences more generally. The question is: what exactly? This question has been debated ever since Darwin (1871) published the Descent of Man, and we appear no closer to resolution of this issue almost 150 years later. Some maintain that evolutionary theory can revolutionize the social sciences, and hence our understanding of human life, by encompassing both the natural and human sciences within a single unifying framework. Wilson's (1975) *Sociobiology* was one of the first, and most emphatic, claims to this effect. Meanwhile, others have resisted the idea of unification, viewing it as little more than imperialist over-reaching by natural scientists (e.g., Rose, 2000).

The question posed by this research topic puts a different, more specific, spin on this issue, asking whether an evolutionary approach within psychology provides a successful alternative to current information-processing and representational views of cognition. The broader issue of unification across the natural and social sciences continues to pervade this more narrow debate, however, because certain proponents of the evolutionary approach insist that the incorporation of the social sciences into the natural sciences is the only means to achieve a coherent understanding of human life. As Tooby and Cosmides (2005) state, evolutionary psychology "in the broad sense, . . . includes the project of reformulating and expanding the social sciences (and medical sciences) in light of the progressive mapping of our species' evolved architecture" (Tooby and Cosmides, 2005, p. 6).

So, what is our answer to this question? The first point to make clear is that any answer we might offer hinges necessarily on the definition of evolutionary psychology that is used. If one settles on a narrow definition, where evolutionary psychology is equated with the views promoted by the "Santa Barbara School", headed by Donald Symons, John Tooby, Leda Cosmides, David Buss, and Steven Pinker (referred to here as Evolutionary Psychology or simply as EP), then the answer is a simple "no" (see also: Dunbar and Barrett, 2007). If one opts instead to define an evolutionary approach in the broadest possible terms (i.e., simply as an evolutionarily informed psychology), then the answer becomes a cautious and qualified "yes."

In what follows, we argue that the primary reason why EP fails as a viable alternative to the standard computational approach is because, in all the important details, it does not differ from this approach. We then go on to suggest that the specific evolutionary arguments in favor of EP, which are used to claim its superiority over other approaches, rest on some rather shaky premises, and cannot be used to rule out alternatives in the way that advocates of EP have supposed. In particular, we deal with arguments relating to the reverse engineering of psychological adaptations, and the logical necessity of domain-specific processes (specifically, arguments relating to the poverty of the stimulus and combinatorial explosion). We then move onto a consideration of recent incarnations of the "massive modularity" hypothesis showing that, while these are not vulnerable to many of the criticisms made against them, it is not clear whether these can, in fact, be characterized as psychological adaptations to past environments. We suggest that, taken together, these arguments weaken the case for EP as the obvious framework for psychology. Finally, we go onto suggest an alternative view of psychological processes, cognitive integration [or the extended mind (EM) hypothesis], that we feel has the potential to improve on the current computational approach; one that is relevant to core areas of psychological research, will promote integration between psychology and other cognate disciplines, but also allow for a healthy pluralism both within psychology and across the social sciences more generally.

THE COMPUTATIONAL CORE OF EVOLUTIONARY PSYCHOLOGY

The primary reason why Evolutionary Psychology cannot offer a successful alternative to computational-representational theories of mind is because it is a computational-representational theory of the mind. Evolutionary Psychology (e.g., Cosmides, 1989; Tooby and Cosmides, 1992, 2005; Cosmides and Tooby, 1994, 1997) is the marriage of "standard" computational cognitive psychology (as exemplified by Chomsky's computational linguistics, e.g., Chomsky, 2005) with the adaptationist program in evolutionary biology (e.g., Williams, 1966); a combination that its proponents cast as revolutionary and capable of producing greater insight, not only into human cognitive processes, but also into the very idea of "human nature" itself (Cosmides, 1989; Tooby and Cosmides, 1992, Cosmides and Tooby, 1994, 1997).

The revolutionary promise of incorporating evolutionary theory into psychology can be traced to, among others, Tooby and Cosmides (1992) conceptual paper on the "psychological foundations of culture," their freely available "primer" on evolutionary psychology (Cosmides and Tooby, 1997), along with Cosmides's (1989) seminal empirical work on an evolved "cheat-detection" module. Another classic statement of how computational theories benefit from the addition of evolutionary theory is Pinker and Bloom's (1990) paper on language as an "instinct," where Chomsky's innate universal grammar was argued to be a product of natural selection (in contrast to Chomsky's own views on the matter).

In all these cases, strong claims are made that leave no doubt that "computationalism" forms the foundation of this approach. Cosmides and Tooby (1997), for example, argue that the brain's evolved function is "information processing" and hence that the brain "is a computer that is made of organic (carbon-based) compounds rather than silicon chips" (paragraph 14), whose circuits have been sculpted by natural selection. More recently, Tooby and Cosmides (2005, p. 16) have stated that "the brain is not just like a computer. It is a computer—that is, a physical system that was designed to process information." While Pinker (2003, pp. 24–27) argues that: "The computational theory of mind ··· is one of the great ideas of intellectual history, for it solves one of the puzzles of the 'mind-body problem' ··· It says that beliefs and desires are information, incarnated as configurations of symbols ··· without the computational theory of mind it is impossible to make sense of the evolution of mind." Accordingly, hypotheses within EP are predicated on the assumption that the brain really is a computational device (not simply a metaphorical one), and that cognition is, quite literally, a form of information processing. In one sense, then, EP cannot offer an improvement on the computational theory of mind because it is premised on exactly this theory. Any improvement on the current state of play must therefore stem from the way in which evolutionary theory is incorporated into this model.

THE EVOLVED COMPUTER

The unique spin that EP applies to the computational theory of mind is that our cognitive architecture is organized into a large number of functionally specialized mechanisms, or "modules," that each performs a specific task (e.g., Tooby and Cosmides, 1992; Cosmides and Tooby, 1997; Barrett and Kurzban, 2006). As these modules are the products of natural selection, they can be considered as "adaptations", or organs of special design, much like the heart or liver. The function of each module is to solve a recurrent problem encountered by our ancestors in the environment of evolutionary adaptedness (EEA), that is, the period over which humans were subject to evolutionary processes, including those of natural selection (Tooby and Cosmides, 1990; Symons, 1992). The EEA therefore represents the sum total of the selection pressures that give rise to a particular adaptation and cannot, strictly speaking, be identified with a particular time or place (Cosmides and Tooby, 1997). In practice, however, based on the argument that, for most of our evolutionary history, humans lived as hunter–gatherers, the EEA is often operationalized to the Pleistocene habitats of East and Southern Africa (although not to any particular location or specific time within this period).

Unlike the notion of computationalism, which is accepted largely without question in psychology and beyond, the concepts of both "massive modularity" and the EEA have met with a large amount of criticism over the years from social and natural scientists alike, as well as from philosophers (e.g., Lloyd, 1999; Buller and Hardcastle, 2000; Rose and Rose, 2000; Buller, 2005; Bolhuis et al., 2011). In general, critics argue that positing modular psychological adaptations to past environments amounts to little more than "just so" story telling, and lacks adequate standards of proof; an accusation that proponents of EP strongly resist and categorically refute (e.g., Holcomb, 1996; Ketelaar and Ellis, 2000; Confer et al., 2010; Kurzban, 2012). As these arguments and counter-arguments have been covered in detail elsewhere (e.g., Conway and Schaller, 2002; Confer et al., 2010), we will not rehearse them again here. Instead, we deal only with those elements that speak to EP's success as a novel computational theory of mind, and its ability to improve on the model we have currently.

CAN WE REVERSE ENGINEER PSYCHOLOGICAL ADAPTATIONS?

Clearly, the success of EP stands or fails by its ability to accurately identify, characterize, and test for psychological adaptations. Within EP, the method of "reverse-engineering" is prominent, and relies heavily on analogies to computational algorithms, functions, inputs, and outputs. In essence, the idea behind reverse-engineering is that one can infer the function of an adaptation from analysis of its form. This involves identifying a problem likely to have been encountered by our ancestors across evolutionary time, and then hypothesizing the kinds of algorithmic "design features" that any psychological adaptation would require in order to solve such a problem. Predictions derived from these hypotheses are then put to the test.

As Gray et al. (2003), among others, have pointed out, such a strategy will work provided all traits are adaptations, that the traits themselves can be easily characterized, and that plausible adaptive hypotheses are hard to come by. Unfortunately, these conditions do not always hold, and identifying adaptations is by no means straightforward. Proponents of EP themselves recognize this problem, acknowledging the existence of both by-products (aspects of the phenotype that are present because they are causally coupled to adaptations) and noise (injected by "stochastic components of evolution"; e.g., Cosmides and Tooby, 1997). Nevertheless, Cosmides and Tooby (1997) argue that, because adaptations are problem-solving machines, it remains possible to identify them "using the same standards of evidence that one would use to recognize a human-made machine: design evidence" (paragraph 65). That is, we are able to identify a machine as a TV rather than a stove by referring to the complex structures that indicate it is good for receiving and transforming electromagnetic waves, and not for cooking food. Thus, if one can show that a phenotypic trait has design features that are complexly specialized for solving an adaptive problem, that these could not have arisen by chance alone, and that their existence is not better explained as the by-product of mechanisms designed to solve some other problem, then one is justified in identifying any such trait as an adaptation (Cosmides and Tooby, 1997).

Although this approach seems entirely reasonable when discussed in these terms, there is ongoing debate as to whether this process is as straightforward as this analysis suggests (particularly with respect to differentiating adaptations from by-products, e.g., Park, 2007). Again, much of this debate turns on the appropriate standard of evidence needed to identify an adaptation, particularly in the case of behavior (see, e.g., Bateson and Laland, 2013). Along with detailed knowledge of the selective environment, it is often argued that evidence for a genetic basis to the trait, along with knowledge of its heritability and its contribution to fitness, are necessary elements in identifying adaptations, not simply the presence of complex, non-random design (see Travis and Reznick, 2009). Defenders of EP counter such arguments by noting, first, that as they are dealing with adaptation, and not current adaptiveness, heritability, and fitness measures are uninformative. By an EP definition, adaptations are traits that have reached fixation. Hence, they should be universal, with a heritability close to zero, and measures of current fitness and the potential for future selection cannot provide any evidence concerning the action of past selection (Symons, 1989, 1990). Second, the argument is made that, given we are willing to accept arguments from design in the case of other species, it is inconsistent and unfair to reject such reasoning in the case of humans. For example, Robert Kurzban, a prominent figure in EP and editor of two main journals in the field, has presented several cogent arguments to this effect in the blog associated with the journal, *Evolutionary Psychology*. In response to a paper presenting the discovery of a "gearing" mechanism in a jumping insect of the genus *Issus*, Kurzban (2013) noted that the authors make a strong claim regarding the evolved function of these interlocking gears (the synchronization of propulsive leg movements). He further noted that that this claim was based on images of the gearing structures alone; there was no reference to the genetic underpinnings or heritability of these structures, nor was there any experimental evidence to establish how the gears work, nor how they contributed to fitness. Kurzban's (2013) point is: if it is permissible for biologists to reason in this way—and to do so persuasively—then why not evolutionary psychologists? (see also Kurzban, 2011b; for a similar example).

On the one hand, this is an entirely fair point. Other things being equal, if evolutionary psychologists and biologists are arguing for the existence of the same phenomena, namely evolutionary adaptations, then the standards of evidence acceptable to one subdiscipline must also be acceptable when used by the other. On the other hand, the phenomena being compared are not quite equivalent. Insect gears are morphological structures, but psychological adaptations are, according to EP, algorithmic processes. Obviously the latter involve morphology at some level, because "all behavior requires underlying physical structures" (Buss, 1999, p. 11), but it is unclear exactly how the psychological mechanism of, say, cheater detection, maps onto any kind of morphological structure within the brain, not least because of the massive degeneracy of neuronal processes (i.e., where many structurally distinct processes or pathways can produce the same outcome). Prinz et al. (2004), for example, modeled a simple motor circuit of the lobster (the stomatogastric ganglion) and were able to demonstrate that there were over 400,000 ways to produce the same pyloric rhythm. In other words, the activity produced by the network of simulated neurons was virtually indistinguishable in terms of outcome (the pyloric rhythm), but was underpinned by a widely disparate set of underlying mechanisms. As Sporns (2011a,b) has suggested, this implies that degeneracy itself is the organizing principle of the brain, with the system designed to maintain its capacity to solve a specific task in a homeostatic fashion. Put simply, maintaining structural stability does not seem central to brain function, and this in turn makes brain function seem much less computer-like.

This, then, has implications for the proponents of EP, who appear to argue for some kind of stable, functionally specialized circuits, even if only implicitly. In other words, the "function from form" argument as applied to EP raises the question of what exactly underlies a "psychological adaptation" if not a morphological structure that can undergo selection? One way around this is to argue that, in line with Marr's (1982) computational theory of vision, EP is concerned only with the computational and algorithmic level of analysis, and not the implementation at the physical level (e.g., Buss, 1999). In other words, EP deals with the computational "cognitive architecture" of the human mind and not with the structure of the wet brain. Hence, as long as a reliable and predictable output is produced from a specified set of inputs, EP researchers are justified in referring to the mechanisms that produce this output as a psychological adaptation (whatever these might be).

This seems to raise another problem, however, in that the reliability and stability of the underlying psychological mechanism is only inferred from the reliability of the behavior produced under a given set of circumstances, and does not involve identification of the actual computational mechanism itself. In physical terms, as was evident from the lobster example, when we consider how an organism's neural circuitry operates in the solving of a task, stability does not seem to be preserved at all, even though virtually indistinguishable network activity is produced as output. If this is true for brains in general and if, as Lehrman (1970) argued, "nature selects for outcomes" and does not particularly care how these are achieved, what has been the target of selection, other than the brain itself? In a sense, one could argue that each specific kind of behavior represents the "modular" component, with a vast number of different neural configurations able to produce it. If so, does this also mean there are a variety of different algorithms as well, and that there is equivalent degeneracy at the algorithmic/representational level? In turn, this raises the issue of whether every possible neural/computational configuration that is capable of producing a given behavior can reasonably be considered a target of selection. Viewed like this, the notion of an "evolved cognitive architecture" comprising specialized circuits devoted to solving a given task serves more as a hypothetical construct used to interpret and make sense of behavioral data, rather than a revealed biological truth. This, of course, does not invalidate the approach—hypothetical constructs are the bread-and-butter of contemporary psychological theorizing—but it does make it difficult to maintain the position that the design argument used to account for stable morphological structures, like insect gears, can be applied equally well to psychological phenomena.

It is important to recognize that our argument is not that there "must be spatial units or chunks of brain tissue that neatly correspond to information-processing units" (Barrett and Kurzban, 2006, p. 641; see also Tooby and Cosmides, 1992). As Barrett and Kurzban (2006) make clear, this does not follow logically, or even contingently, from the argument that there are specialized processing modules; functional networks can be widely distributed across the brain, and not localized to any specific region (Barton, 2007). Rather, we are questioning the logic that equates morphological with psychological structure, given recent neurobiological findings (assuming, of course, that these findings are general to all brains). If neural network structure is both degenerate and highly redundant because the aim is to preserve functional performance in a dynamic environment, and not to form stable representational structures based on inputs received, then it becomes less easy to draw a direct analogy between morphological structures and cognitive "structures."

The computational metaphor does, however, lend itself to such an analogy, and is perhaps the reason why the structure–function argument seems so powerful from an EP point of view. That is, when the argument is couched in terms of "machinery in the human mind" or "cognitive architecture," psychological phenomena are more readily conceptualized as stable, physical structures (of some or other kind) that are "visible" to selection. If they are seen instead as temporally and individually variable neuronal configurations that converge on reliable behavioral outputs without any stable circuits, as Prinz et al. (2004) demonstrated in the lobster, a shift of focus occurs, and the brain itself is revealed as the complex adaptation we seek. The capacity to produce frequency-dependent, condition-dependent behavior then becomes the realized expression of the complex adaptation that is the brain, rather than these capacities themselves being seen as distinct adaptations.

This does not end the matter, of course, because we still need to understand how highly active degenerate brain circuits can produce flexible behavior. This is an unresolved empirical issue that cannot be tackled by theoretical speculation alone. Rather, we are simply placing a question mark over the idea that it is possible to identify psychological adaptations at the cognitive level, via behavioral output, without any consideration of how these are physically implemented. Given that, according to EP's own argument, it is the physical level at which selection must act, and this is what permits an analogy to be drawn with morphological structures, then if brains are less computer-like and representational than we thought, the idea that psychological adaptations can be viewed as stable algorithmic mechanisms that run on the hardware of the brain may also require some re-thinking.

EVOLVED, LEARNED, AND EVOLVED LEARNING CAPACITIES

Another, more positive, corollary of questioning the premise that the brain is a computer with highly specialized, evolved circuits, is that there is less temptation to distinguish between evolved and learned behaviors in ways that generate a false dichotomy. Although Evolutionary Psychologists do not deny the importance of learning and development – indeed there are some who actively promote a "developmental systems" approach (as we discuss below)—the fundamental assumption that the human cognitive system is adapted to a past environment inevitably results in the debate being framed in terms of evolved versus learned mechanisms. When, for example, the argument is made that humans possess an evolved mating psychology, or an evolved cheater detection mechanism, there is the implicit assumption that these are not learned in the way we ordinarily understand the term, but are more akin to being "acquired" in the way that humans are said to acquire language in a Chomskyan computational framework: we may learn the specifics of our particular language, but this represents a form of "parameter setting," rather than the formation of a new skill that emerges over time. To be clear, Evolutionary Psychologists recognize that particular kinds of "developmental inputs" are essential for the mechanism to emerge—there is no sense in which psychological modules are argued to be "hard-wired" and impervious to outside input—but there is the denial that these mechanisms reflect the operation of domain-general learning principles being applied in a particular environmental context (Tooby and Cosmides, 1992; Cosmides and Tooby, 1997; Buss, 1999; Barrett and Kurzban, 2006).

In contrast, some researchers take the view that development is more than just "tuning the parameters" of modular capacities via specific inputs, but that development involves dynamic change over time in a highly contingent fashion (e.g., Karmiloff-Smith, 1995, 1998; Smith and Thelen, 2003). In this constructivist view, our ability to engage in certain kinds of reasoning about particular domains of interest, such as cheater detection, emerges through the process of development itself. Hence, these kinds of reasoning are likely to be specific to our time and place and may be very different to the kinds of reasoning performed by our ancestors in both the recent and more distant past. These criticisms are often combined with those mentioned above, namely that the evidence for evolved modular mechanisms is not particularly convincing, and is consistent with alternative explanations for the same data. That is, opponents of modular EP argue that we may learn many of the things that EP attributes to evolved psychological adaptations. In this way, learned mechanisms end up being opposed to those that have evolved.

Such an opposition is, however, false because all learning mechanisms, whether general or domain-specific, have evolved, and therefore what is learned is never independent of evolutionary influences. This is something that both critics and proponents of EP alike recognize, and yet the opposition of evolved versus culturally learned behavior continually arises (e.g., Pinker, 2003). Perhaps this is because the argument is framed in terms of adaptation, when the real issue being addressed by both parties is the degree to which there are constraints on our ability to learn, that is, the degree of plasticity or flexibility shown by our learning mechanisms. Evolutionary Psychologists, in essence, argue simply that all humans converge on a particular suite of mechanisms that once enhanced the fitness of our ancestors, through a process of learning that is heavily guided by certain biological predispositions.

DOES FLEXIBILITY REQUIRE SPECIFICITY?

This is not to say, however, that humans lack flexibility. Indeed, the argument from EP is precisely that "a brain equipped with a multiplicity of specialized inference engines" will be able to "generate sophisticated behavior that is sensitively tuned to its environment." (Cosmides and Tooby, 1997, paragraph 42). What it argues against, rather, is the idea that the mind resembles a "blank slate" and that its "evolved architecture consists solely or predominantly of a small number of general purpose mechanisms that are content-independent, and which sail under names such as 'learning,' 'induction,' 'intelligence,' 'imitation,' 'rationality,' 'the capacity for culture,' or simply 'culture.'" (Cosmides and Tooby, 1997, paragraph 9). This view is usually characterized as the "standard social science model" (SSSM), where human minds are seen as 'primarily (or entirely)' free social constructions" (Cosmides and Tooby, 1997, paragraph 10), such that the social sciences remain disconnected from any natural foundation within evolutionary biology. This is because, under the SSSM, humans are essentially free to learn anything and are thus not constrained by biology or evolutionary history in any way (Cosmides and Tooby, 1997).

Tooby and Cosmides's (1992) attack on the SSSM is used to clear a space for their own evolutionary theory of the mind. Their argument against the SSSM is wide-ranging, offering a detailed analysis of what they consider to be the abject failure of the social sciences to provide any coherent account of human life and behavior. As we do not have space to consider all their objections in detail (most of which we consider ill-founded), we restrict ourselves here to their dismissal of "blank slate" theories of learning, and the idea that a few domain-general processes cannot suffice to produce the full range of human cognitive capacities.

The first thing to note is that Tooby and Cosmides's (1992) argument against the SSSM bears a striking resemblance to Chomsky's (1959) (in)famous dismissal of Skinner's work. This similarly attempted to undercut the idea of general learning mechanisms and replace it with notions of domain-specific internal structure. This similarity is not surprising, given that Tooby and Cosmides (1992) expressly draw on Chomsky's logic to make their own argument. What is also interesting, however, is that, like Chomsky (1959), Tooby and Cosmides (1992), and Cosmides and Tooby (1997) simply assert the case against domain-general mechanisms, rather than provide empirical evidence for their position. As such, both Chomsky's dismissal of radical behaviorism and Evolutionary Psychology's dismissal of the SSSM amount to "Hegelian arguments." This is a term coined by Chemero (2009) based on Hegel's assertion, in the face of contemporary evidence to the contrary, that there simply could not be a planet between Mars and Jupiter (actually an asteroid) because the number of planets in the solar system was necessarily seven, given the logic of his own theoretical framework: an eighth planet was simply impossible, and no evidence was needed to support or refute this statement. In other words, Hegelian arguments are those that rule out certain hypotheses *a priori*, solely through the assertion of particular theoretical assumptions, rather than on the basis of empirical data.

In the case of behaviorism, we have Chomsky's famous "poverty of the stimulus" argument, which asserted, purely on the basis of "common sense" rather than empirical evidence, that environmental input was too underdetermined, too fragmentary, and too variable to allow any form of associative learning of language to occur. Hence, an innate language organ or "language acquisition device" was argued to fill the gap. Given the alternative was deemed impossible on logical grounds, the language acquisition device was thus accepted by default. The Hegelian nature of this argument is further revealed by the fact that empirical work on language development has shown that statistical learning plays a much larger role than anticipated in language development, and that the stimulus may be much "wealthier" than initially imagined (e.g., Gómez, 2002; Soderstrom and Morgan, 2007; Ray and Heyes, 2011).

Similarly, the argument from EP is that a few domain-general learning mechanisms cannot possibly provide the same flexibility as a multitude of highly specialized mechanisms, each geared to a specific task. Thus, a content-free domain-general cognitive architecture can be ruled out a priori. Instead, the mind is, in Tooby and Cosmides' (1992) famous analogy, a kind of Swiss Army knife, with a different tool for each job. More recently, the metaphor has been updated by Kurzban (2011a), who uses the iPhone as a metaphor for the human mind, with its multitude of "apps," each fulfilling a specific function.

Rather than demonstrating empirically that domain-general psychological mechanisms cannot do the job asked of them, this argument is instead supported by reference to functional specialization in other organ systems, like the heart and the liver, where different solutions are needed to solve two different problems: pumping blood and detoxifying poisons. Of course, the brain is also a functionally specialized organ that helps us coordinate and organize behavior in a dynamic, unpredictable world. Using the same logic, this argument is extended further, however, to include the idea that our psychological architecture, which is a product of our functionally specialized brain, should also contain a large number of specialized "mental organs," or "modules," because a small number of general-purpose learning mechanisms could not solve the wide variety of adaptive problems that we face; we need different cognitive tools to solve different adaptive problems. Analogies are also drawn with functional localization within the brain: visual areas deal only with visual information, auditory areas deal only with auditory information, and so on.

THE POVERTY OF THE STIMULUS REVISITED

Cosmides and Tooby (1994) use their own version of Chomsky's poverty of stimulus argument to support this claim for domain-specificity (see also Frankenhuis and Ploeger, 2007 for further discussion) suggesting that "adaptive courses of action can be neither deduced nor learned by general criteria alone because they depend on statistical relationships between features of the environment, behavior, and fitness that emerge over many generations and are, therefore, not observable during a single lifetime alone." Thus, general learning mechanisms are ruled out, and modular evolved mechanisms deemed necessary, because these "come equipped with domain-specific procedures, representations or formats prepared to exploit the unobserved" (p. 92).

Using the example of incest avoidance to illustrate this point, Cosmides and Tooby (1994) argue that only natural selection can "detect" the statistical patterns indicating that incest is maladaptive, because " ... it does not work by inference or simulation. It takes the real problem, runs the experiment, and retains those design features that lead to the best available outcome" (p. 93). Frankenhuis and Ploeger (2007), state similarly: "to *learn* that incest is maladaptive, one would have to run a long-term epidemiological study on the effects of in-breeding: produce large numbers of children with various related and unrelated partners and observe which children fare well and which don't. This is of course unrealistic" (p. 700, emphasis in the original). We can make use of Samuels' (2002, 2004) definition of "innateness" to clarify matters further. According to Samuels' (2002, 2004), to call something "innate" is simply to say that it was not acquired by any form of psychological process. Put in these terms, Cosmides and Tooby's (1994) and Frankenhuis and Ploeger's (2007) argument is that, because it is not possible to use domain-general psychological mechanisms to learn about the long-term fitness consequences of incest, our knowledge must be innate in just this sense: we avoid mating with close relatives because we have a functionally specialized representational mechanism that acts as a vehicle for domain-specific knowledge about incest, which was acquired by a process of natural selection. Note that domain-specificity of this kind does not automatically imply innateness, as Barrett and Kurzban (2006) and Barrett (2006) make clear. Here, however, the argument does seem to suggest that modules must contain some specific content acquired by the process of natural selection alone, and not by any form of learning, precisely because the latter has been ruled out on a priori grounds.

On the one hand, these statements are entirely correct—a single individual cannot literally observe the long-term fitness consequences of a given behavior. Moreover, there is evidence to suggest that humans do possess a form of incest avoidance mechanism, the Westermarck effect, which results in reduced sexual interest between those raised together as children (Westermarck, 1921; also see Shepher, 1971; Wolf, 1995). On the other hand, it is entirely possible for humans to learn with whom they can and cannot mate, and how this may be linked to poor reproductive outcomes—indeed, people can and do learn about such things all the time, as part of their upbringing, and also as part of their marriage and inheritance systems. Although it is true that many incest taboos do not involve biological incest as such (these are more concerned with wealth concentration within lineages), it is the case that mating and marriage with close relatives is often explicitly forbidden and codified within these systems. Moreover, the precise nature of incest taboos may shift over time and space. Victorian England, for example, was a veritable hotbed of incestuous marriage by today's standards (Kuper, 2010); indeed, Darwin himself, after famously making a list of the pros and cons of marriage, took his first cousin as his wife.

It is also apparent that, in some cases, shifts in how incestuous unions are defined often relate specifically to the health and well-being of children produced. Durham (2002), for example, discusses the example of incest (or *rual*) among the Nuer cattle herders of Sudan, describing how differing conceptions of the incest taboo exist within the population, such that people obey or resist the taboo depending on their own construal of incest. As a result, some couples become involved in incestuous unions, and may openly challenge the authority of the courts, running off together to live as a family. When these events occur, they are monitored closely by all and if thriving children are produced, the union is considered to be "fruitful" and "divinely blessed." Hence, in an important sense, such unions are free of *rual* (this is partly because the concept of *rual* refers to the hardships that often result from incest; indeed, it is the *consequences* of incest that are considered morally reprehensible, and *not* the act itself). Via this form of "pragmatic fecundity testing," the incest taboo shifts over time at both the individual and institutional level, with local laws revised to reflect new concepts of what constitutes an incestuous pairing (Durham, 2002).

This example is presented neither to deny the existence of the Westermarck effect (see Durham, 1991 for a thorough discussion of the evidence for this), nor to dispute that there are certain statistical patterns that are impossible for an individual to learn over the course of its lifetime. Rather it is presented to demonstrate that humans can and do learn about fitness-relevant behaviors within their own lifetimes, and can make adaptive decisions on this basis. Personal knowledge of the outcomes from long-term epidemiological study is not needed necessarily because humans can call on the accumulated stores of inter-generational knowledge residing in, and available from, other members of their community. This can be knowledge that is passed on in folklore, stories, and songs, as well as prohibitions and proscriptions on behavior set down in custom and law. As the Nuer example illustrates, we also form our own ideas about such things, regardless of what we learn from others, possibly because people can, in fact, tap into the "long-term epidemiological study" set up by the evolutionary process a long time ago, and which has been running for many years. It would indeed be impossible to learn the pattern required if each individual had to set up his or her own individual experiment at the point at which they were ready to mate, but people potentially can see the outcomes of the "long term study" in the failed conceptions of others. Furthermore, the Nuer example also makes clear that we are capable of updating our existing knowledge in the light of new evidence. Given that any such learning abilities are themselves evolved, there is no suggestion here that incest taboos are free from any kind of biological influence, and are purely socially constructed. What we are suggesting, however, is that this example undermines the notion that domain-general mechanisms cannot, even in principle, do the job required. We agree that an individual who lives for around 70 years cannot learn the outcome of a process that may take several generations to manifest, but this is a completely different issue from whether an individual can learn that certain kinds of matings are known to have deleterious consequences, and what to do about them. Thus, one cannot use this argument as *a priori* proof that evolved content-rich domain-specific mechanisms are the only possible way that adaptive behavior can be brought about.

In other words, this is not an argument specifically about the mechanisms by which we avoid incest, but a general argument against the strategy used to establish the necessity of evolved domain-specific processes: positing that individuals cannot learn the actual fitness consequences of their actions, as defined within evolutionary biology, does not mean that humans are unable to learn to pick up on more immediate cues that reflect the relative costs and benefits that do accrue within a lifetime (cues that may well be correlated with long-term fitness) and then use these to guide their own behavior and that of their descendants. We suggest it is possible for our knowledge of such matters to be acquired, at least partly, by a psychological process during development. Hence, it is not "innate." Moreover, even if it could be established that domain-specific innate knowledge was needed in a particular domain (like incest), this does not mean that it can be used as an argument to rule out general learning processes across all adaptive problem domains.

In addition to the above examples, Heyes (2014) has recently presented a review of existing data on infants, all of which were used to argue for rich, domain-specific interpretations of "theory of mind" abilities, and shows that these results can also be accounted for by domain-general processes. Heyes and colleagues also provide their own empirical evidence to suggest that so-called "implicit mentalizing ability" could also equally well be explained by domain-general processes, such as those related to attentional orienting (Santiesteban et al., 2013). In addition, Heyes (2012) has suggested that certain cognitive capacities, which have been argued to be evolved, specialized social learning mechanisms that permit transmission of cultural behaviors, may themselves be culturally-inherited learned skills that draw on domain-general mechanisms.

One point worth noting here is that, if data interpreted as the operation of domain-specific processes can be equally well accounted for by domain-general process, then this has important implications for our earlier discussion of "reverse engineering" and inferring evidence of design, as well as for the necessity of domain-specialization. As Durham (1991) suggested, with respect to the issue of incest taboos: "the influence of culture on human phenotypes will be to produce adaptations that appear as though they could equally well have evolved by natural selection of alternative genotypes . . . cultural evolution can mimic the most important process in genetic microevolution" (p. 289). Therefore, even if a good case could be made that a cognitive process looks well-designed by selection, an evolved module is not the only possible explanation for the form such a process takes.

THE PARADOX OF CHOICE?

These demonstrations of the power of domain-general learning are interesting because Tooby and Cosmides (1992) also attempt to rule this out on the basis of "combinatorial explosion," which they consider to be a knock-down argument. They state that, without some form of structure limiting the range of options open to us, we would become paralyzed by our inability to work through all possible solutions to reach the best one for the task at hand. This again seems to be something of a Hegelian argument, for Tooby and Cosmides (1992) simply assert that "[If] you are limited to emitting only one out of 100 alternative behaviors every successive minute, [then] after the second minute you have 10,000 different behavioral sequences from which to choose, a million by the third minute, a trillion by six minutes" with the result that "The system could not possibly compute the anticipated outcome of each alternative and compare the results, and so must be precluding without complete consideration the overwhelming majority of branching pathways" (p. 102).

This formulation simply assumes that any sequence of behavior needs to be planned ahead of time before being executed, and that an exponential number of decisions *have* to made, whereas it is also possible for behavioral sequences to be organized prospectively, with each step contingent on the previous step, but with no requirement for the whole sequence to be planned in advance. That is, one can imagine a process of Bayesian learning, with an algorithm that is capable of updating its "beliefs." Relatedly, Tooby and Cosmides (1992) apparently assume that each emission of behavior is an independent event (given the manner in which they calculate probabilities) when, in reality, there is likely to be a large amount of auto-correlation, with the range of possible subsequent behaviors being conditional on those that preceded it.

Finally, Tooby and Cosmides's (1992) argument assumes that that there is no statistical structure in the environment that could be used to constrain the range of options available (e.g., something akin to the affordances described by Gibson (1966, 1979), and that organisms are thus required to compute all contingencies independently of the environment. May et al. (2006), however, have shown that robotic rat pups, provided with a completely random control architecture (i.e., without any rules at all, whether domain-general or domain-specific), were nevertheless able to produce the distinctive huddling behavior of real rat pups, due to the constraining influence of bodily and environmental structures. That is, rather than having to decide among a trillion different options, according to the logic described above, bodily and environmental structures allow for complex behavior to emerge without any decision-making at all. Thus, there is no reason, in principle, to suppose that humans could not be similarly scaffolded and guided by environmental constraints, in ways that would allow general-learning mechanisms to get a grip and, over time, produce functionally specialized mechanisms that help guide behavior. Indeed, this may also be one reason why human infant learning mechanisms take the form they do, with only a limited capacity at first, so as not to overwhelm the system. As Elman (1993) showed, in his classic paper on infant language learning, the training of a neural network succeeded only when such networks were endowed with a limited working memory, and then gradually "matured." More recently, Pfeifer and Bongard (2007) have reported on similar findings relating to the development of behavior in a "babybot."

Thus, while reasonable when taken at face value, many of the arguments offered in support of an evolved domain-specific computational architecture turn out to be rather Hegelian on closer inspection, rather than well-supported by empirical data. As such, the increased value of evolutionary psychology remains an open issue: it is not clear that EP offers an improvement over other computational perspectives that do not make strong claims for an evolved, domain-specific architecture of this kind.

MODULES 2.0

The contention that EP has sometimes offered Hegelian arguments should not be taken to suggest that opponents of the EP position are not guilty of the same. We do not deny that modular accounts have also been ruled out based on assertion rather than evidence, and that there have been many simplistic straw man arguments about genetic determinism and reductionism. Interestingly enough, Jerry Fodor himself, author of "The Modularity of Mind" (Fodor, 1983), asserted that it was simply impossible for "central" cognitive processes to be modular, and Fodor (2000) also presents several Hegelian arguments against the evolutionary "massive modularity" hypothesis. Indeed, the prevalence of such arguments in the field of cognitive science is Chemero's (2009) main reason for raising the issue. His suggestion is that, unlike older disciplines, cognitive science gives greater credence to Hegelian arguments because it has yet to establish a theoretical framework and a supporting body of data that everyone can agree is valid. This means that EP does not present us with the knock-down arguments against the SSSM and domain-general learning that it supposes, but neither should we give Hegelian arguments against EP any credence for the same reason.

As both Barrett and Kurzban (2006) and Frankenhuis and Ploeger (2007) have documented, many of the misrepresentations and errors of reasoning concerning the massive modularity hypothesis in EP can, for the most part, be traced precisely to the conflation of Fodor's (1983) more limited conception of modularity with that of Tooby and Cosmides (1992, 2005) and Cosmides and Tooby (1994). Criticisms relating to encapsulation, cognitive impenetrability, automaticity, and neural localization are not fatal to the EP notion of modularity because EP's claim is grounded in functional specialization, and not any specific Fodorian criterion; criticisms that argue in these terms therefore miss their mark (Barrett and Kurzban, 2006).

Given that most criticisms of the massive modularity hypothesis prove groundless from an EP point of view, it is worth considering Barrett and Kurzban's (2006) analysis in detail in order to understand exactly what the EP view of modularity entails, and whether this updated version of the modularity argument is more convincing in terms of presenting an improved alternative to standard computational models.

First and foremost, Barrett and Kurzban (2006) make clear that functional specialization *alone* is the key to understanding modularity from an EP point of view, and domain-specific abilities, and hence modules, "should be construed in terms of the formal properties of information that render it processable by some computational procedure" (Barrett and Kurzban, 2006, p. 634). That is, modules are defined by their specialized input criteria and their ability to handle information in specialized ways: only information of certain types can be processed by the mechanism in question. Natural selection's role is then "to shape a module's input criteria so that it processes inputs from the proper domain in a reliable, systematic and specialized fashion." (By "proper" domain they mean the adaptive problem, with its associated array of inputs, that the module has been designed by selection to solve; this stands in contrast to the "actual" domain, which includes the range of inputs to which the module is potentially able to respond, regardless of whether these were present ancestrally: see Sperber, 1994; Barrett and Kurzban, 2006, p. 635). Hence, the domain-specificity of a module is a natural consequence of its functional specialization (Barrett and Kurzban, 2006). Crudely speaking, then, modules are defined more in terms of their syntactic rather than semantic properties—they are not "content domains," but more like processing rules.

Barrett and Kurzban (2006) argue that their refinement of the modularity concept holds two implications. First, given that a module is defined as any process for which it is possible to formally specify input criteria, there is no sharp dividing line between domain-specific and domain-general processes, because the latter can also be defined in terms of formally specified input criteria. The second, related implication is that certain processes, like working memory, which are usually regarded as domain-general (i.e., can process information from a wide variety of domains, such as flowers, sports, animals, furniture, social rituals), can also be considered as modular because they are thought to contain subsystems with highly specific representational formats and a sensitivity only to specific inputs (e.g., the phonological loop, the visuospatial sketchpad; Barrett and Kurzban, 2006). This does, however, seem to deviate slightly from Cosmides and Tooby's (1997) suggestion that modules are designed to solve particular adaptive problems encountered by our ancestors: what *specific* adaptive problem does "working memory" solve, given that the integration of information seems common to all adaptive problems? (see also Chiappe and Gardner, 2012).

Taken on its own terms, however, Barrett and Kurzban's (2006) definition of modularity should raise no objections from anyone committed to the computational theory of mind, nor does it come across as particularly radical with respect to its evolutionary theorizing. Thus, Barrett and Kurzban (2006) dissolve many of the problems identified with massive modularity, and suggest that most criticisms are either misunderstandings or caricatures of the EP position. When considered purely as a computational theory (i.e., leaving to one side issues relating to the EEA, and Hegelian arguments relating to the need for evolved domain-specific knowledge), the more recent EP position is thereby revealed as both reasonable and theoretically sophisticated.

DEVELOPMENTAL CONSIDERATIONS: "SOFT" DEVELOPMENTAL SYSTEMS THEORY AND EP

It is also important to note that the more recent work in EP also incorporates a strongly developmental perspective, again laying rest to criticisms that EP is overly determinist and that EP researchers are prone to simplistic claims about the innateness or "hard-wiring" of particular traits (e.g., Barrett, 2006; Frankenhuis et al., 2013). In particular, work by Barrett (2006) and Frankenhuis et al. (2013) attempts to integrate developmental systems theory (DST) into EP. This represents an encouraging move at first glance, because the aim of DST is to moves us away from a dichotomous account of development, where two classes of resources—genes and "all the rest"—interact to produce the adult phenotype, toward an account in which there is no division into two fundamentally different kinds of resources. Instead, genes are seen as just one resource among many available to the developmental process, and are not the central drivers of the process (Griffiths and Gray, 1994). Indeed, genes can play their role only if all other resources essential for development are in place. This should not be taken to mean that all resources contribute equally to each and every process, and always assume the same relative importance: the aim is not to "homogenize" the process of development, and obliterate the distinctions between different kinds of resources, but to call into question the way in which we divide up and classify developmental resources, opening up new ways to study such processes.

The EP take on DST, however, is self-confessedly "soft," and continues to maintain that standard distinction between genetic and environmental resources. As defined by Frankenhuis et al. (2013), "soft DST" regards developmental systems as "dynamic entities comprising genetic, molecular, and cellular interactions at multiple levels, which are shaped by their external environments, but distinct from them" (p. 585). Although a strongly interactionist view, the "developmental system" here remains confined to the organism alone, and it continues to treat genetic influences as fundamentally distinct from other developmental resources, with a unique role in controlling development. More pertinently, Barrett (2006) suggests that, precisely because it gets us away from any kind of "genetic blueprint" model of growth and development, it may be "fruitful to think of developmental processes themselves in computational terms: they are designed to take inputs, which include the state of the organism and its internal and external environments as a dynamically changing set of parameters, and generate outputs, which are the phenotype, the end-product of development. One can think of this end-product, the phenotype, as the developmental target" (p. 205). Thus, once again, EP does not present us with an alternative to current computational models, because, as Barrett (2006) makes clear, the incorporation of these additional theories and models into an EP account entails a reinterpretation of such theories in fully computational terms.

ANCIENT ADAPTATIONS OR THOROUGHLY MODERN MODULES?

Another consideration we would like to raise is whether, as a result of incorporating a clearly articulated developmental component, EP researchers actually undermine some of their own claims regarding the evolved domain-specificity of our putative modular architecture. Barrett (2006), for example, uses Sperber's (1994) ideas of actual and proper domains to good effect in his developmental theorizing, distinguishing clearly between "types" of cognitive processes (which have been the target of selection) and "tokens" of these types (which represent the particular manner in which this manifests under a given set of conditions). This enables him to provide a cogent account of an evolved modular architecture that is capable of generating both novelty and flexibility. The interesting question, from our perspective, is whether the modules so produced can be still be considered adaptations to past environments, as Cosmides and Tooby (1994, 1997) insist must be the case.

For example, as Barrett (2006) notes, many children possess the concept of *Tyrannosaurus rex*, which we know must be evolutionarily novel because, as a matter of empirical fact, there has been no selection on humans to acquire this concept. Nevertheless, as Barrett (2006) argues, we can consider the possession of this concept as a token outcome that falls well within the proper type of a putative predator-recognition system. This argument is logical, sensible, and difficult to argue with, yet seems at odds with the central idea presented in much of Tooby and Cosmides (1992, 2005) work that the modular architecture of our minds is adapted to a past that no longer exists. That is, as tokens of a particular type of functional specialization, produced by a developmental process that incorporates evolutionarily novel inputs, it would seem that any such modules produced are, in fact, attuned to present conditions, and not to an ancestral past. As Barrett (2006) notes, Inuit children acquire the concept of a polar bear, whereas Shuar children acquire the concept of a jaguar, even though neither of these specific animals formed part of the ancestral EEA; while the mechanisms by which these concepts are formed, and why these concepts are formed more easily than others, may well have an evolutionary origin, the actual functional specializations produced – the actual tokens produced within this proper type – would seem to be fully modern. The notion that "our modern skulls house a stone age mind" (Cosmides and Tooby, 1997) or that, as Pinker (2003, p. 42) puts it; "our brains are not wired to cope with anonymous crowds, schooling, written language, governments, police courts, armies, modern medicine, formal social institutions, high technology and other newcomers to the human experience" are thus undermined by the token-type distinction developed in more recent EP theorizing.

One could argue, perhaps, that what Pinker means here is that our brains did not evolve to deal with such things specifically, i.e., that he is simply making Barrett's (2006) argument that these phenomena are just tokens of the various types that our brains *are* wired to cope with. But, if this is the case, then it seems that EP loses much of its claim to novelty. If it is arguing only that humans have evolved psychological mechanisms that develop in ways that attune them to their environment, this does not differ radically from computational cognitive theories in human developmental and comparative psychology more generally.

This sounds like a critical argument, but we do not mean it in quite the way it sounds. Our argument is that the theoretical EP literature presents a perfectly acceptable, entirely conventional computational theory, one that admits to novelty, flexibility, the importance of learning and development, and incorporates the idea that a species' evolutionary history is important in shaping the kinds of psychological processes it possesses and the ease with which they are acquired. Our point is that this is no different from the arguments and empirical findings offered against behaviorism toward the middle of the last century, which heralded the rise of cognitive psychology (see e.g., Malone, 2009; Barrett, 2012). Central to all cognitivist psychological theories is the idea that there are internal, brain-based entities and processes that transform sensory input into motor output, and the acknowledgment that much of this internal structure must reflect a past history of selection. EP, in this sense then, is not controversial within psychology, and is entirely consonant with current psychological theory and practice. Thus, in addition to the fact that EP is based on the same computational metaphor as standard cognitive psychology, it is also apparent that most of the evolutionary aspects of this theory, as reconceived by current authors, do not render it revolutionary within psychology, nor is there any reason to believe that the remaining social sciences should view EP as any more essential or necessary to their work than current computational models. Indeed, one could simply take the message of EP to be that, as with all species, humans are prepared to learn some things more readily than others as a result of evolving within a particular ecological niche. Seen in these terms, it is surprising that EP continues to be considered controversial within psychology, given that its more recent theoretical claims can be seen as entirely mainstream.

AN ALTERNATIVE SUGGESTION: COGNITIVE INTEGRATION

If our conclusion is that EP does not offer an alternative to standard computational cognitive psychology, we are left with two further questions: Is an alternative really needed? And if so, what is it? In the remainder of this paper, we tackle these questions in turn.

One reason why we might need an alternative to standard computational and representational theories of mind is because, despite claims to the contrary (e.g., Pinker, 2003), it has yet to provide a complete account of how humans and other species produce adaptive, flexible behavior in a dynamic, unpredictable world. Although we may understand something about capacities like playing chess, engaging in formal reasoning, or natural language (i.e., tasks that involve the manipulation of symbols according to rules, and are inherently computational anyway), we still lack a good understanding of the more mundane tasks that characterize much of what we could call "everyday" intelligence, such as how we manage to negotiate uneven terrain or coordinate all the actions and objects necessary to make a pot of tea, or coordinate our social actions with others when we dance, engage in conversation smoothly and easily, or simply walk down a crowded street.

It is also interesting to note that the computational metaphor also hindered the advancement of robotics in much the same way. The MIT roboticist and inventor of the Roomba, Rodney Brooks, relates how his first formal foray into robotics was at Stanford, where they took a "classic" artificial intelligence approach, with robots that took in sensory inputs, computed solutions to a task based on these inputs, and then executed them. This made the robots operate very slowly, even to the extent that the movement of the sun across the sky, and the changes in the shadows thrown, had the ability to confuse their internal representations. Only by moving away from a classic computational "sense–represent–plan–act" approach, and eliminating the need for internal representations altogether, was progress made (Brooks, 2002; also see Pfeifer and Bongard, 2007).

In other words, the idea that cognition is, ultimately, a form of "mental gymnastics" (Chemero, 2009) involving the construction, manipulation, and use of internal representations according to a set of rules does not seem to provide an adequate account of how humans and other animals achieve most of the activities they engage in every day. Given this, the obvious alternatives to the standard computational theories of mind are the various forms of "E-cognition" (embodied, embedded, enactive, extended, and extensive) that have been gaining steady ground in recent years within cognitive science and philosophy of mind and, to a lesser extent, psychology itself, both theoretically and empirically (e.g., Clark, 1997, 2008; Gallagher, 2005; Wheeler, 2005; Menary, 2007, 2010; Pfeifer and Bongard, 2007; Chemero, 2009; Barrett, 2011; Hutto and Myin, 2013). While these approaches vary in the degree to which they reject computational and representational approaches to cognition [e.g., Clark (1997, 2008) argues for a form of "dynamic computationalism," whereas Hutto and Myin (2013) reject any suggestion that "basic minds," i.e., those that are non-linguistic, make use of representational content], they have in common the idea that body and environment contribute to cognitive processes in a constitutive and not merely causal way; that is, they argue that an organism's cognitive system extends beyond the brain to encompass other bodily structures and processes, and can also exploit statistical regularities and structure in the environment.

For reasons of space, we cannot provide a full account of these alternatives, and the similarities and differences between them. Instead, we will focus on one particular form of E-cognition, the "EM" hypothesis. Specifically, we will deal with "second-wave EM" thinking, also known as "cognitive integration," as exemplified by the work of Clark (2008), Sutton (2010), and Menary (2007, 2010). We believe this supplies the beginnings of an answer to why an alternative to standard computational theory is required, and illustrates why EP cannot provide it.

Put simply, the EM hypothesis is that external resources and artifacts, like written language and other forms of material culture, are central to the production of the modern human cognitive phenotype, and serve to augment and ratchet up the power of our evolved brains (e.g., Clark, 1997, 2008; Menary, 2007, 2010; Sutton, 2010). External resources are argued to play a role in a cognitive process in ways that are either functionally equivalent to that carried out by a biological brain such that, for the duration of that process, the external resource can be considered to be part of the cognitive system (the so-called "parity principle": Clark and Chalmers, 1998) or they play roles that are complementary to brain-based processes, and augment them accordingly (the "complementarity principle": Menary, 2007, 2010; Sutton, 2010). We can see this in everything from the way in which our ability to multiply very large numbers is enhanced by the use of pencil and paper to the fascinating literature on sensory substitution devices, where blind individuals are able to visually explore their environments via external devices that supply auditory or tactile information in ways that compensate for the loss of their visual sense (Bach-y-Rita et al., 1969, 2003; Bach-y-Rita and Kercel, 2003). The idea here, then, is not to eliminate all distinctions between different kinds of resources and consider them to be synonymous, but to reduce our prejudice that only internal processes taking place in the brain count as cognitive, and to redraw the boundaries of the cognitive system accordingly. The notion of the EM or cognitive integration therefore dissolves the boundary between brain, body, and world, and rejects the idea that the "cognitive system" of an animal is confined to its brain alone (for a review of how cognitive integration relates to the non-human animal literature, see Barrett, 2011). Instead, as Clark (1997) and Clark and Chalmers (1998) suggested, many of our cognitive states can be considered as hybrids, distributed across biological and non-biological realms. We are, as the title of one of Clark's books suggests, "natural born cyborgs" (Clark, 2003).

CULTIVATING THE HYBRID HUMAN

The human cognitive system, in particular, is extended far beyond that of other species because of the complex interaction between the biological brain and body, and the wide variety of artifacts, media and technology that we create, manipulate, and use. It is crucial to realize that the hybrid nature of human beings is not a recent phenomenon tied to the development of modern technology. On the contrary, cognitive extension is a process that has been taking place ever since the first hominin crafted the first stone tools, and has continued apace ever since. What this means today is that, as Clark (2003) puts it, "our technologically enhanced minds are barely, if at all, tethered to the ancestral realm" (p. 197) nor are they now "constrained by the limits of the on-board apparatus that once fitted us to the good old savannah" (p. 242). This stands in stark contrast to the EP position, where the only "cognitive machinery" involved is the brain itself, whose structure is tied fundamentally and necessarily to the past, untouched by our culturally constructed, technological world. As Tooby and Cosmides (1992) put it: "what mostly remains, once you have removed from the human world everything internal to humans, is the air between them" (p. 47). Cognitive integration begs to differ in this regard, and invites us to look around and see that this simply cannot be true.

Consequently, our view is that cognitive integration promises to explain more about human psychology than EP ever could because it forces a stronger recognition of the historical, sociocultural nature of human psychology — the fact that we develop in a socially and culturally rich milieu that reflects the contingent nature of both historical and evolutionary events. Past generations structure the developmental context of those that succeed them, providing resources that are essential to the production of species-typical behavior. Importantly, however, they also enhance what can be achieved by providing ever more sophisticated forms of cognitive scaffolding that itself augments the scaffolding that previous generations bequeathed to them (Sterelny, 2003; Stotz, 2010). This can be seen as something akin to the process of ecological succession, where the engine of change is the organism's own impact on the environment; a metaphor we have stolen from Griffiths and Gray's (1994) treatment of DST. Indeed, there is a natural sympathy between DST as an approach to the study of the evolution and development of biological organisms, and the more dynamical forms of E-cognition that adopt a similar approach to the evolution, development, and functioning of cognitive systems. In particular, Stotz (2010) argues convincingly that understanding human psychology from an evolutionary perspective requires a focus on "developmental niche construction"; an idea that, as the name suggests, incorporates elements of both developmental systems and niche construction theory (see also Griffiths and Stotz, 2000). Understanding modern human psychology therefore requires an understanding of the entanglement of our technologies, cultural practices, and historical events with our evolutionary heritage, and not the reverse engineering of human cognitive architecture alone. Clark (2002) suggests that the pay-off from this kind of expanded psychology "... could be spectacular: nothing less than a new kind of cognitive scientific collaboration involving neuroscience, physiology and social, cultural and technological studies in equal measure" (p. 154).

Turning to an embodied, extended approach as an alternative to standard computational theories, including that of EP, is a step in the right direction not only because it recognizes the hybrid nature of humans, in the terms described above, but also in the sense discussed by Derksen (2005), who argues that a recognition of ourselves as part-nature and part-culture creates a distinct and interesting boundary (or rather a range of related boundaries) between humans and the natural world. As Derksen (2005) points out, the reflexive ways in which we deal with ourselves and our culture are very different from our dealings with the natural world, and a recognition of our hybrid nature allows us to explore these boundaries in their own right, and to examine how and why these may shift over time (for example, issues relating to fertility treatments, stem cell research, cloning, and organ transplantation all raise issues concerning what is "natural" versus "unnatural," and how we should conceive of human bodies in both moral and ethical terms).

To emphasize this shifting, dynamic element of the boundaries we straddle as hybrid natural-cultural beings, Derksen (2005) uses the metaphor of "cultivation." Like a gardener tending his plants, humans cultivate their nature, and in so doing elaborate their potential. As Vygotsky (1962) suggested, this makes culture something we do, rather than something that happens to us, or that we simply possess. The intersection between cognitive integration and cultivation should be clear, for cognitive integration, which naturally takes into account our historical, social, cultural, and evolutionary underpinnings in equal measure, is key to our ability to cultivate new forms of human nature (see also Bakhurst, 2011). Indeed, proponents of cognitive integration, suggest that "human nature" continually emerges in an ongoing way from human activity, and that we cannot pinpoint some fixed and unchanging essence (Derksen, 2012). As Wheeler and Clark (2008) put it: "our fixed nature is a kind of meta-nature . . . an extended cognitive architecture whose constancy lies mainly in its continual openness to change" (p. 3572).

Such a view stands in contrast to the EP perspective, where the idea of a universal human nature, comprising our evolved computational architecture, is a central premise of the approach. The problem here, as we see it, is that cultural variation across time and space is seen simply as the icing on the cake of our evolved universal psychology. Humans are argued to manifest different behaviors under different conditions because our evolved architecture works rather like a jukebox that can play different records given different inputs; what Tooby and Cosmides (1992) refer to as "evoked culture." By this definition, such cultural differences fail to penetrate or alter our "human nature" in any fundamental way. Such a view also fails to account for how and why completely different modes of thinking have emerged over space and time as a consequence of the invention of different material artifacts, like the wheel, the plow, time-pieces, accounting systems, and written language. Such things are not evoked simply by exposure to local ecological conditions, and their existence fundamentally changes how we think about the world (without the invention of time-pieces, for example, the cultural importance of timeliness and punctuality so valued by, among others, the Swiss and Germans, would not, and could not, be considered any part of human nature). EP therefore leaves out the most distinctive aspect of human cognitive life—the way in which material culture is both a cause and consequence of our psychological and cultural variability—whereas cognitive integration makes this the central element to understanding why humans think and act in the ways that they do (Menary, 2010; Sutton, 2010; Malafouris, 2013).

Finally, as Derksen (2005, 2007) argues, a view of human nature as a matter of cultivation, as a form of ongoing human activity, renders the idea of unification between the biological and social sciences wrongheaded on its face: the very diversity of disciplines in which we engage reflects the disunity, the boundary between nature and culture, that characterizes our humanity, and not the fundamental "psychic unity" of humankind that EP assumes. Consequently, there is a very real need to collaborate and confront each other along disciplinary boundaries, but not dissolve, ignore, or erase them (Derksen, 2005, 2007). Such sentiments are echoed by those involved in the study of cognitive integration, who similarly call for this kind of multidisciplinary pluralism in our approach to the study of human nature and the mind (Derksen, 2005, 2007; Menary, 2007; Clark, 2008; Wheeler and Clark, 2008; Menary, 2010; Sutton, 2010). Simply put, our hybrid selves can be studied in no other way.

ACKNOWLEDGMENTS

Louise Barrett is supported by the Canada Research Chairs (Tier 1) Program and NSERC Discovery grants. Thomas V. Pollet is supported by NWO (Veni, 451.10.032). Gert Stulp is supported by an NWO Rubicon grant. We are grateful to Maarten Derksen for reading and commenting on an earlier draft of the manuscript, and for the comments of our two reviewers. Thanks also to Danielle Sulikowski for inviting us to contribute to this research topic.

REFERENCES

Bach-y-Rita, P., Collins, C. C., Saunders, F. A., White, B., and Scadden, L. (1969). Vision substitution by tactile image projection. *Nature* 221, 963–964. doi: 10.1038/221963a0

Bach-y-Rita, P., Tyler, M. E., and Kaczmarek, K. A. (2003). Seeing with the brain. *Int. J. Hum. Comput. Interact.* 15, 285–295. doi: 10.1207/S15327590IJHC1502_6

Bach-y-Rita, P., and W Kercel, S. (2003). Sensory substitution and the human–machine interface. *Trends Cogn. Sci.* 7, 541–546. doi: 10.1016/j.tics.2003.10.013

Bakhurst, D. (2011). *The Formation of Reason.* Oxford: Wiley-Blackwell. doi: 10.1002/9781444395600

Barrett, H. C. (2006). "Modularity and design reincarnation," in *The Innate Mind: Culture and Cognition*, eds P. Carruthers, S. Laurence, and S. P. Stich (Oxford: Oxford University Press), 199–217.

Barrett, H. C., and Kurzban, R. (2006). Modularity in cognition: framing the debate. *Psychol. Rev.* 113, 628–647. doi: 10.1037/0033-295X.113.3.628

Barrett, L. (2011). *Beyond the Brain: How Body and Environment Shape Animal and Human Minds.* Princeton, NJ: Princeton University Press.

Barrett, L. (2012). "Why behaviorism isn't satanism," in *The Oxford Handbook of Comparative Evolutionary Psychology*, eds J. Vonk and T. K. Shackelford (Oxford: Oxford University Press), 17–38.

Barton, R. A. (2007). "Evolution of the social brain as a distributed neural system," in *Oxford Handbook of Evolutionary Psychology*, eds L. Barrett and R. I. M. Dunbar (Oxford: Oxford University Press), 129–144.

Bateson, P., and Laland, K. N. (2013). Tinbergen's four questions: an appreciation and an update. *Trends Ecol. Evol.* 28, 712–718. doi: 10.1016/j.tree.2013.09.013

Bolhuis, J. J., Brown, G. R., Richardson, R. C., and Laland, K. N. (2011). Darwin in mind: new opportunities for evolutionary psychology. *PLoS Biol.* 9:e1001109. doi: 10.1371/journal.pbio.1001109

Brooks, R. A. (2002). *Robot: The Future of Flesh and Machines.* London: Allen Lane.

Buller, D. J. (2005). *Adapting Minds: Evolutionary Psychology and the Persistent Quest for Human Nature.* Cambridge, MA: MIT Press. doi: 10.1002/evan.1360040603

Buller, D. J., and Hardcastle, V. (2000). Evolutionary psychology, meet developmental neurobiology: against promiscuous modularity. *Brain Mind* 1, 307–325. doi: 10.1023/A:1011573226794

Buss, D. M. (1999). *Evolutionary Psychology: The New Science of the Mind.* Needham Heights, MA: Allyn & Bacon.

Chemero, A. (2009). *Radical Embodied Cognitive Science.* Cambridge, MA: MIT Press.

Chiappe, D., and Gardner, R. (2012). The modularity debate in evolutionary psychology. *Theory Psychol.* 22, 669–682. doi: 10.1177/0959354311398703

Chomsky, N. (1959). A review of BF Skinner's Verbal Behavior. *Language (Baltim.)* 35, 26–58. doi: 10.2307/411334

Chomsky, N. (2005). Three factors in language design. *Linguist. Inq.* 36, 1–22. doi: 10.1162/0024389052993655

Clark, A. (1997). *Being There: Putting Brain, Body, and World Together Again.* Cambridge, MA: MIT Press.

Clark, A. (2002). Towards a science of the bio-technological mind. *Int. J. Cogn. Technol.* 1, 21–33. doi: 10.1075/ijct.1.1.03cla

Clark, A. (2003). *Natural-Born Cyborgs: Minds, Technologies, and the Future of Human*. Oxford: Oxford University Press.

Clark, A. (2008). *Supersizing the Mind: Embodiment, Action, and Cognitive Extension*. Oxford: Oxford University Press. doi: 10.1093/acprof:oso/9780195333213.001.0001

Clark, A., and Chalmers, D. (1998). The extended mind. *Analysis* 58, 7–19. doi: 10.1093/analys/58.1.7

Confer, J. C., Easton, J. A., Fleischman, D. S., Goetz, C. D., Lewis, D. M. G., Perilloux, C., et al. (2010). Evolutionary psychology. Controversies, questions, prospects, and limitations. *Am. Psychol.* 65, 110–126. doi: 10.1037/a0018413

Conway, L. G., and Schaller, M. (2002). On the verifiability of evolutionary psychological theories: an analysis of the psychology of scientific persuasion. *Pers. Soc. Psychol. Rev.* 6, 152–166. doi: 10.1207/S15327957PSPR0602_04

Cosmides, L. (1989). The logic of social exchange: has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition* 31, 187–276. doi: 10.1016/0010-0277(89)90023-90021

Cosmides, L., and Tooby, J. (1994). "Origins of domain specificity: the evolution of functional organization," in *Mapping the Mind: Domain Specificity in Cognition and Culture*, eds L. A. Hirschfeld and S. A. Gelman (Cambridge: Cambridge University Press), 85–116. doi: 10.1017/CBO9780511752902.005

Cosmides, L., and Tooby, J. (1997). *Evolutionary Psychology: A Primer*. Available at: http://www.cep.ucsb.edu/primer.html (accessed May 08, 2014).

Darwin, C. (1871). *The Descent of Man and Selection in Relation to Sex*. London: John Murray. doi: 10.1037/12293-000

Derksen, M. (2005). Against integration why evolution cannot unify the social sciences. *Theory Psychol.* 15, 139–162. doi: 10.1177/0959354305051360

Derksen, M. (2007). Cultivating human nature. *New Ideas Psychol.* 25, 189–206. doi: 10.1016/j.newideapsych.2006.09.001

Derksen, M. (2012). Human nature as a matter of concern, care, and cultivation. *Paper Presented at Symposium on The Adapted Mind*, Ghent.

Dunbar, R. I. M., and Barrett, L. (2007). "Evolutionary psychology in the round," in *Oxford Handbook of Evolutionary Psychology*, eds R. Dunbar and L. Barrett (Oxford: Oxford University Press), 3–9.

Durham, W. H. (1991). *Coevolution: Genes, Culture, and Human Diversity*. Stanford, CA: Stanford University Press.

Durham, W. H. (2002). "Cultural variation in time and space: the case for a populational theory of culture," in *Anthropology Beyond Culture*, eds R. G. Fox and B. J. King (Oxford: Berg), 193–206.

Elman, J. L. (1993). Learning and development in neural networks: the importance of starting small. *Cognition* 48, 71–99. doi: 10.1016/0010-0277(93)90058-4

Fodor, J. A. (1983). *The Modularity of Mind: An Essay on Faculty Psychology*. Cambridge, MA: MIT Press.

Fodor, J. A. (2000). *The Mind Doesn't Work That Way: The Scope and Limits of Computational Psychology*. Cambridge, MA: MIT Press.

Frankenhuis, W. E., Panchanathan, K., and Barrett, C. H. (2013). Bridging developmental systems theory and evolutionary psychology using dynamic optimization. *Dev. Sci.* 16, 584–98. doi: 10.1111/desc.12053

Frankenhuis, W. E., and Ploeger, A. (2007). Evolutionary psychology versus fodor: arguments for and against the massive modularity hypothesis. *Philos. Psychol.* 20, 687–710. doi: 10.1080/09515080701665904

Gallagher, S. (2005). *How the Body Shapes the Mind*. Cambridge: Cambridge University Press. doi: 10.1093/0199271941.001.0001

Gibson, J. J. (1966). *The Senses Considered as Perceptual Systems*. Boston, MA: Houghton Mifflin.

Gibson, J. J. (1979). *The Ecological Approach to Visual Perception*. Boston, MA: Houghton Mifflin.

Gómez, R. L. (2002). Variability and detection of invariant structure. *Psychol. Sci.* 13, 431–436. doi: 10.1111/1467-9280.00476

Gray, R. D., Heaney, M., and Fairhall, S. (2003). "Evolutionary psychology and the challenge of adaptive explanation," in *From Mating to Mentality: Evaluating Evolutionary Psychology*, eds K. Sterelny and J. Fitness (Hove: Psychology Press), 247–268.

Griffiths, P. E., and Gray, R. D. (1994). Developmental systems and evolutionary explanation. *J. Philos.* 91, 277–304. doi: 10.2307/2940982

Griffiths, P. E., and Stotz, K. (2000). How the mind grows: a developmental perspective on the biology of cognition. *Synthese* 122, 29–51. doi: 10.1023/A:1005215909498

Heyes, C. (2012). Grist and mills: on the cultural origins of cultural learning. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 367, 2181–2191. doi: 10.1098/rstb.2012.0120

Heyes, C. (2014). False belief in infancy: a fresh look. *Dev. Sci.* doi: 10.1111/desc.12148 [Epub ahead of print].

Holcomb, H. R. III (1996). Just so stories and inference to the best explanation in evolutionary psychology. *Minds Mach.* 6, 525–540.

Hutto, D. D., and Myin, E. (2013). *Radicalizing Enactivism: Basic Minds Without Content*. Cambridge, MA: MIT Press.

Karmiloff-Smith, A. (1995). *Beyond Modularity: A Developmental Perspective on Cognitive Science*. Cambridge, MA: MIT Press.

Karmiloff-Smith, A. (1998). Development itself is the key to understanding developmental disorders. *Trends Cogn. Sci.* 2, 389–398. doi: 10.1016/S1364-6613(98)01230-1233

Ketelaar, T., and Ellis, B. J. (2000). Are evolutionary explanations unfalsifiable? Evolutionary psychology and the Lakatosian philosophy of science. *Psychol. Inq.* 11, 1–21. doi: 10.1207/S15327965PLI1101_01

Kuper, A. (2010). *Incest and Influence: The Private Life of Bourgeois England*. Cambridge, MA: Harvard University Press.

Kurzban, R. (2011a). *Is Your Brain Like an Iphone?* Available at: http://www.psychologytoday.com/blog/mind-design/201101/is-your-brain-iphone (accessed May 10, 2014).

Kurzban, R. (2011b). *Two Sides of the Same Coyne*. Available at: http://www.epjournal.net/blog/2011/01/two-sides-of-the-same-coyne/ (accessed May 10, 2014).

Kurzban, R. (2012). "Just so stories are (bad) explanations," *Functions are Much Better Explanations*. Available at: http://www.epjournal.net/blog/2012/09/just-so-stories-are-bad-explanations-functions-are-much-better-explanations/ (accessed May 8, 2014).

Kurzban, R. (2013). *How Do Biologists Support Functional Claims?* Available at: http://www.epjournal.net/blog/2013/09/how-do-biologists-support-functional-claims/ (accessed May 14, 2014).

Lehrman, D. S. (1970). "Semantic and conceptual issues in the nature-nurture problem," in *Development and Evolution of Behavior: Essays in Memory of T. C. Schneirla*, eds L. R. Aronson, E. Tobach, D. S. Lehrman, and J. S. Rosenblatt (San Francisco, CA: Freeman), 17–52.

Lloyd, E. A. (1999). Evolutionary psychology: the burdens of proof. *Biol. Philos.* 14, 211–233. doi: 10.1023/A:1006638501739

Malafouris, K. (2013). *How Things Shape the Mind: A Theory of Material Engagement*. Cambridge, MA: MIT Press.

Malone, J. C. (2009). *Psychology: Pythagoras to Present*. Cambridge, MA: MIT Press. doi: 10.1002/cplx.20149

Marr, D. (1982). *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information*. New York, NY: Henry Holt. doi: 10.1057/9780230592889

May, C. J., Schank, J. C., Joshi, S., Tran, J., Taylor, R. J., and Scott, I.-E. (2006). Rat pups and random robots generate similar self-organized and intentional behavior. *Complexity* 12, 53–66. doi: 10.1002/cplx.20149

Menary, R. A. (2007). *Cognitive Integration: Mind and Cognition Unbounded*. London: Palgrave Macmillan.

Menary, R. A. (2010). "Cognitive integration and the extended mind," in *The Extended Mind*, ed. R. A. Menary (Cambridge, MA: MIT Press), 227–243.

Park, J. H. (2007). Distinguishing byproducts from non-adaptive effects of algorithmic adaptations. *Evol. Psychol.* 5, 47–51. doi: 10.1017/S0140525X00081061

Pfeifer, R., and Bongard, J. (2007). *How the Body Shapes the Way We Think: A New View of Intelligence*. Cambridge, MA: MIT Press. doi: 10.1038/nn1352

Pinker, S. (2003). *The Blank Slate: The Modern Denial of Human Nature*. London: Penguin.

Pinker, S., and Bloom, P. (1990). Natural language and natural selection. *Behav. Brain Sci.* 13, 707–727. doi: 10.1017/S0140525X00081061

Prinz, A. A., Bucher, D., and Marder, E. (2004). Similar network activity from disparate circuit parameters. *Nat. Neurosci.* 7, 1345–1352. doi: 10.1038/nn1352

Ray, E., and Heyes, C. (2011). Imitation in infancy: the wealth of the stimulus. *Dev. Sci.* 14, 92–105. doi: 10.1111/j.1467-7687.2010.00961.x

Rose, H. (2000). "Colonising the social sciences," in *Alas, Poor Darwin: Arguments Against Evolutionary Psychology*, eds H. Rose and S. Rose (London: Jonathan Cape), 106–128.

Rose, H., and Rose, S. (2000). *Alas, Poor Darwin: Arguments Against Evolutionary Psychology*. London: Jonathan Cape.

Samuels, R. (2002). Nativism in cognitive science. *Mind Lang.* 17, 233–265. doi: 10.1111/1468-0017.00197

Samuels, R. (2004). Innateness in cognitive science. *Trends Cogn. Sci.* 8, 136–141. doi: 10.1016/j.tics.2004.01.010

Santiesteban, I., Catmur, C., Coughlan Hopkins, S., Bird, G., and Heyes, C. (2013). Avatars and arrows implicit mentalizing or domain-general processing? *J. Exp. Psychol. Hum. Percept. Perform.* 39, 1–9. doi: 10.1037/a0035175

Shepher, J. (1971). Mate selection among second generation kibbutz adolescents and adults: incest avoidance and negative imprinting. *Arch. Sex. Behav.* 1, 293–307. doi: 10.1007/BF01638058

Smith, L. B., and Thelen, E. (2003). Development as a dynamic system. *Trends Cogn. Sci.* 7, 343–348. doi: 10.1016/S1364-6613(03)00156-156

Soderstrom, M., and Morgan, J. L. (2007). Twenty-two-month-olds discriminate fluent from disfluent adult-directed speech. *Dev. Sci.* 10, 641–653. doi: 10.1111/j.1467-7687.2007.00605.x

Sperber, D. (1994). "The modularity of thought and the epidemiology of representations.," in *Mapping the Mind: Domain Specificity in Cognition and Culture*, eds L. A. Hirschfeld and S. A. Gelman (Cambridge: Cambridge University Press), 39–67. doi: 10.1017/CBO9780511752902.003

Sporns, O. (2011a). *Networks of the Brain*. Cambridge, MA: MIT Press.

Sporns, O. (2011b). The human connectome: a complex network. *Ann. N. Y. Acad. Sci.* 1224, 109–125. doi: 10.1111/j.1749-6632.2010.05888.x

Sterelny, K. (2003). *Thought in a Hostile World: The Evolution of Human Cognition*. Oxford: Blackwell.

Stotz, K. (2010). Human nature and cognitive-developmental niche construction. *Phenom. Cogn. Sci.* 9, 483–501. doi: 10.1007/s11097-010-9178-7

Sutton, J. (2010). "Exograms and interdisciplinarity: history, the extended mind, and the civilizing process," in *The Extended Mind*, ed. R. A. Menary (Cambridge, MA: MIT Press), 189–225.

Symons, D. (1989). A critique of Darwinian anthropology. *Ethol. Sociobiol.* 10, 131–144. doi: 10.1016/0162-3095(89)90016-2

Symons, D. (1990). Adaptiveness and adaptation. *Ethol. Sociobiol.* 11, 427–444. doi: 10.1016/0162-3095(90)90019-3

Symons, D. (1992). "On the use and misuse of Darwinism in the study of human behavior," in *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, eds J. H. Barkow, L. Cosmides, and J. Tooby (Oxford: Oxford University Press), 137–162.

Tooby, J., and Cosmides, L. (1990). The past explains the present: emotional adaptations and the structure of ancestral environments. *Ethol. Sociobiol.* 11, 375–424. doi: 10.1016/0162-3095(90)90017-Z

Tooby, J., and Cosmides, L. (1992). "The psychological foundations of culture," in *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, eds J. H. Barkow, L. Cosmides, and J. Tooby (Oxford: Oxford University Press), 19–136.

Tooby, J., and Cosmides, L. (2005). "Conceptual foundations of evolutionary psychology," in *The Handbook of Evolutionary Psychology*, ed. D. M. Buss (New York, NY: Wiley), 5–67.

Travis, J., and Reznick, D. N. (2009). "Adaptation," in *Evolution: The First Four Billion Years*, eds M. Ruse, and J. Travis (Cambridge, MA: Harvard University Press), 105–131.

Vygotsky, L. S. (1962). *Thought and Language*. Cambridge, MA: MIT Press. doi: 10.1037/11193-000

Westermarck, E. (1921). *The History of Human Marriage*, 5th Edn. London: Macmillan.

Wheeler, M. (2005). *Reconstructing the Cognitive World: The Next Step*. Cambridge, MA: MIT Press.

Wheeler, M., and Clark, A. (2008). Culture, embodiment and genes: unravelling the triple helix. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 363, 3563–3575. doi: 10.1098/rstb.2008.0135

Williams, G. C. (1966). *Adaptation and Natural Selection*. Princeton, NJ: Princeton University Press.

Wilson, E. O. (1975). *Sociobiology: The New Synthesis*. Cambridge, MA: Harvard University Press.

Wolf, A. P. (1995). *Sexual Attraction and Childhood Association: A Chinese Brief for Edward Westermarck*. Stanford, CA: Stanford University Press.

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 20 May 2014; accepted: 21 July 2014; published online: 12 August 2014.

*Citation: Barrett L, Pollet TV and Stulp G (2014) From computers to cultivation: reconceptualizing evolutionary psychology. Front. Psychol. **5**:867. doi: 10.3389/fpsyg.2014.00867*

This article was submitted to Evolutionary Psychology and Neuroscience, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

GENERAL COMMENTARY
published: 21 November 2014
doi: 10.3389/fpsyg.2014.01348

Our computational nature: comment on Barrett et al.

John Klasios*

York University, Toronto, ON, Canada
**Correspondence: john.klasios@gmail.com*

Edited by:
J. Michael Williams, Drexel University, USA

Reviewed by:
Aaron T. Goetz, California State University, Fullerton, USA

Keywords: evolutionary psychology, computationalism, human nature, computers, cognitive science

A commentary on

From computers to cultivation: reconceptualizing evolutionary psychology
by Barrett, L., Pollet, T. V., and Stulp, G. (2014). Front. Psychol. 5:867. doi: 10.3389/fpsyg.2014.00867

I argue that Barrett et al. (2014) have misinterpreted evolutionary psychologists' notion of computation. Barrett et al. seemingly presume that the notion of computation deployed by evolutionary psychologists (e.g., Pinker, 1997; Tooby and Cosmides, 2005) is tantamount to positing a *physical* architecture whose form of computation proceeds via the syntactic-like transformations of spatially discrete representational symbols or sentence-like structures—i.e., in the manner of a Turing machine. But this is simply not the notion of computation that evolutionary psychologists advocate (in spite of the fact that a Turing machine architecture, for instance, is nonetheless compatible with it).

The notion of computation is philosophically complex, with many different meanings and a multifaceted history (Piccinini, 2012). By "computation," evolutionary psychologists fundamentally mean to say that the brain evolved to compute in the generic sense of the term. This more generic notion of computation, and its relation to a physical substrate, is outlined by Pinker (2005):

> "Computation" … does not refer to what a commercially available digital computer does but to a more generic notion of mechanical rationality … . In this conception, a computational system is one in which knowledge and goals are represented as *patterns* in bits of matter ("representations"). (p. 2, emphasis added)

The misunderstanding of what evolutionary psychologists mean by computation also leads Barrett et al. to view various other conceptions of cognition—i.e., embodied, embedded, extended, enactive—as alternatives to the computational approach when, in actuality, they can easily be seen as complementary to it. For evolutionary psychologists are primarily focused on the functional level of analysis of psychological adaptations rather than their physical instantiations (i.e., their causal–physical basis in the brain, body, and wider environment). And this focus on the functional level of analysis allows researchers to investigate psychological adaptations in a manner that abstracts away from their instantiations in the brain, body, and larger context (i.e., ecological) in which they are embedded. The modular, computational framework of evolutionary psychology is quite compatible with, and can be meaningfully situated within, an overall physical and causal account that is highly complex, widely distributed, and highly diffuse. So, far from invalidating or highlighting a "prejudice" inherent to computationalism or evolutionary psychology, the supposed alternative approach that Barrett et al. advocate is rather a difference of focus and emphasis. For there is nothing within the theoretical approach of evolutionary psychology that in principle denies the existence of the kinds of "E-cognition" that Barrett et al. draw attention to. At a pragmatic level, different research programs will simply find it profitable to have differing explanatory focuses and emphases.

Barrett et al. also raise skepticism regarding the relationship between psychological adaptations and their neurobiological underpinnings. But it is important to note that the form–function fit that evolutionary psychologists focus on qua adaptationists pertains most directly to aspects of "psychological design" rather than to properties of the neurobiological realization of those designs. Thus, the reverse-engineering approach accordingly homes in on the psychological level of analysis and not the neurobiological one (or at least not primarily). More generally, at this stage of the game it is premature to draw overly strict conclusions on precisely how psychological adaptations may or may not be instantiated in the brain—e.g., if and how they are "multiply realizable" by neurobiological bases, and whether to interpret neuroimaging results according to a regionally-focused or network-wide perspective, etc. (e.g., Klein, 2012; Colombo, 2013).

Barrett and colleagues' discussion of human nature is also problematic. For instance, they endorse Wheeler and Clark's (2008) conception of human nature as "a kind of meta-nature … an extended cognitive architecture whose constancy lies mainly in its continual openness to change" (p. 3572) and lead the reader to believe that it is necessarily at variance with the notion of human nature alluded to by evolutionary psychologists. On the contrary, however, evolutionary psychologists recognize this underlying constancy and refer to it as our underlying "developmental programs" (e.g., Tooby et al., 2003). For evolutionary psychologists, human nature is tantamount to the ontogenesis of our species-typical psychological adaptations. On this view, human nature is envisioned as being expressed through development in ways that are guided, generative, and constrained. The precise details of how guided, generative, and constrained this underlying nature is are of course a complex empirical matter that has barely just commenced, scientifically speaking. At any rate, abstractly modeling postulated psychological adaptations in computational terms is an invaluable method of investigation (see Barrett, 2006, 2007; Bechtel, 2007; Tooby and Cosmides, 2008; Frankenhuis et al., 2013; Levy and Bechtel, 2013).

Indeed, evolutionary psychologists argue that our developmental programs should be computationally mapped in ever-increasing detail, ultimately yielding a high-resolution map of human nature. Barrett et al. claim that human nature can be "cultivated," shaped, and refracted (etc.). But the extent to which this is possible is ultimately an empirical question, and the more we can understand the nature of our developmental programs, the less need we will have for such vague notions. And in any case, however much we can cultivate our developmental programs, they are fundamentally a product of past selection and thus cannot be adapted—in the *adaptationist* sense—to present and future conditions (e.g., Tooby and Cosmides, 1990).

Barrett et al. also crucially omit certain aspects of evolutionary psychologists' treatment of culture. To wit, Barrett et al. imply that evolutionary psychologists cannot account for the way in which material artifacts, beliefs, and so forth, interact with the underlying developmental programs undergirding our species-typical cognitive architecture. To the contrary: evolutionary psychologists' notion of epidemiological culture refers both to the transmission of culture between individual minds and its impact on the cognitive architecture of those minds (Tooby and Cosmides, 1992; Sperber, 1996). Furthermore, models of epidemiological culture can, in principle, be as complex and dynamic as need be. Hence, the allegations by Barrett et al. that evolutionary psychology is inconsistent with or fails in principle to account for such cultural phenomena are baseless.

ACKNOWLEDGMENT

Thanks to Aaron Goetz for the useful comments.

REFERENCES

Barrett, H. C. (2006). "Modularity and design reincarnation," in *The Innate Mind: Volume 2: Culture and Cognition*, eds P. Carruthers, S. Laurence, and S. Stich (New York, NY: Oxford University Press), 199–217.

Barrett, H. C. (2007). "Development as the target of evolution: a computational approach to developmental systems," in *The Evolution of Mind: Fundamental Questions and Controversies*, eds S. W. Gangestad and J. A. Simpson (New York, NY: The Guilford Press), 186–192.

Barrett, L., Pollet, T. V., and Stulp, G. (2014). From computers to cultivation: reconceptualizing evolutionary psychology. *Front. Psychol.* 5:867. doi: 10.3389/fpsyg.2014.00867

Bechtel, W. (2007). "Reducing psychology while maintaining its autonomy via mechanistic explanation," in *The Matter of the Mind: Philosophical Essays on Psychology, Neuroscience and Reduction*, eds M. Schouten and H. Looren de Jong (Oxford: Basil Blackwell), 172–198.

Colombo, M. (2013). Moving forward (and beyond) the modularity debate: a network perspective. *Philos. Sci.* 80, 356–377. doi: 10.1086/670331

Frankenhuis, W. E., Panchanathan, K., and Barrett, H. C. (2013). Bridging developmental systems theory and evolutionary psychology using dynamic optimization. *Dev. Sci.* 16, 584–598. doi: 10.1111/desc.12053

Klein, C. (2012). Cognitive ontology and region- versus network-oriented analyses. *Philos. Sci.* 79, 952–960. doi: 10.1086/667843

Levy, A., and Bechtel, W. (2013). Abstraction and the organization of mechanisms. *Philos. Sci.* 80, 241–261. doi: 10.1086/670300

Piccinini, G. (2012). "Computationalism," in *The Oxford Handbook of Philosophy of Cognitive Science*, eds E. Margolis, R. Samuels, and S. P. Stich (New York, NY: Oxford University Press), 222–249.

Pinker, S. (1997). *How the Mind Works.* New York, NY: Norton.

Pinker, S. (2005). So how does the mind work? *Mind Lang.* 20, 1–24. doi: 10.1111/j.0268-1064.2005.00274.x

Sperber, D. (1996). *Explaining culture: a naturalistic approach.* Oxford: Blackwell.

Tooby, J., and Cosmides, L. (1990). The past explains the present: emotional adaptations and the structure of ancestral environments. *Ethol. Sociobiol.* 11, 375–424.

Tooby, J., and Cosmides, L. (1992). "The psychological foundations of culture," in *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, eds J. H. Barkow, L. Cosmides, and J. Tooby (New York, NY: Oxford University Press), 19–136.

Tooby, J., and Cosmides, L. (2005). "Conceptual foundations of evolutionary psychology," in *The Handbook of Evolutionary Psychology*, ed D. M. Buss (Hoboken, NJ: John Wiley & Sons), 5–67.

Tooby, J., and Cosmides, L. (2008). "The evolutionary pscyhology of the emotions and their relationship to internal regulatory variables," in *Handbook of Emotions, 3rd Edn.*, eds M. Lewis, J. M. Haviland-Jones, and L. F. Barrett (New York, NY: Guilford), 114–137.

Tooby, J., Cosmides, L., and Barrett, H. C. (2003). The second law of thermodynamics is the first law of psychology: evolutionary developmental psychology and the theory of tandem, coordinated inheritances: Comment on Lickliter and Honeycutt (2003). *Psychol. Bull.* 129, 858–865. doi: 10.1037/0033-2909.129.6.858

Wheeler, M., and Clark, A. (2008). Culture, embodiment and genes: unravelling the triple helix. *Philos. Trans. R. Soc. B Biol. Sci.* 363, 3563–3575. doi: 10.1098/rstb.2008.0135

Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 20 September 2014; accepted: 05 November 2014; published online: 21 November 2014.

Citation: Klasios J (2014) Our computational nature: comment on Barrett et al. Front. Psychol. **5***:1348. doi: 10.3389/fpsyg.2014.01348*

This article was submitted to Evolutionary Psychology and Neuroscience, a section of the journal Frontiers in Psychology.

frontiers in
PSYCHOLOGY

OPINION ARTICLE
published: 28 November 2014
doi: 10.3389/fpsyg.2014.01372

The uniquely predictive power of evolutionary approaches to mind and behavior

Ian D. Stephen*, Mehmet K. Mahmut, Trevor I. Case, Julie Fitness and Richard J. Stevenson

Department of Psychology, Macquarie University, Sydney, NSW, Australia
**Correspondence: ian.stephen@mq.edu.au*

Edited by:
Danielle Sulikowski, Charles Sturt University, Australia

Reviewed by:
Gad Saad, Concordia University, Canada

Keywords: evolutionary psychology, e-cognition, ethology, explanatory power, proximate/ultimate

INTRODUCTION

Barrett et al. (2014) argue that the primary contribution of evolutionary psychology (EP), as defined by the Santa Barbara school (Cosmides and Tooby, 1987; see also Laland and Brown, 2011) is the conception of the mind as a collection of separate, domain-specific mental modules that evolved to solve specific adaptive problems. This, they argue, means that EP does not represent a true alternative to computational models of mind and is therefore not a significant advance on more traditional cognitive approaches. Instead, they recommend that e-cognition, and in particular the concept of the extended mind, can best enhance our understanding of human mind and behavior. While we appreciate Barrett et al.'s enthusiasm for an interesting and relatively new approach to understanding mind and behavior, we argue here that, independent of the veracity of the concept of massive modularity (which is an empirical question; Barrett et al., 2014; Burke, 2014; Stephen, 2014), an evolutionary approach provides a substantial advance in the understanding of mind and behavior. Here, we make two main arguments. First, we argue that a full understanding of mind, brain and behavior requires the consideration of all four of Tinbergen's levels of explanation, which can only be achieved by approaching the problem through the lens of evolution (independent of the assumption of massive, domain-specific modularity, or of any other model). Second, we argue that the embodied cognition approach advocated by Barrett et al. (2014) is actually better understood as an extension of traditional *causal* (mechanistic), and *ontogenetic* (developmental) approaches than as a revolutionary approach in its own right, and therefore is best examined through the lens of evolution.

THE VALUE OF EVOLUTIONARY APPROACHES TO MIND AND BEHAVIOR

In what is now widely considered the foundational document of human ethology, Niko Tinbergen makes the case that behavior can be addressed at four different explanatory levels (Tinbergen, 1963). In addition to the *causal* (or mechanistic) and *ontogenetic* (developmental) levels of explanation that are typical of modern psychology, Tinbergen proposed that a full understanding of behavior requires that we consider two additional, evolutionary levels of explanation. The *phylogenetic* level considers the evolutionary history of the behavior, and the *functional* level considers what he calls the survival value, or what modern evolutionists would call the fitness value or selective value of the behavior (though more recently, O'Brien and Gallup, 2011, have suggested that the role of culture represents a fifth level of explanation). While Barrett et al. (2014) assert that the primary advance offered by EP is the conception of the mind as massively modular, we suggest that the defining feature of evolutionary approaches to psychology is simply the application of the evolutionary concepts of selection and fitness to human behavior. This approach allows us to address human psychology through Tinbergen's *phylogenetic* and *functional* levels of explanation, providing novel hypotheses and a more thorough understanding of the subject. Despite rarely being acknowledged directly, these principles are applied in a range of evolutionary approaches to mind and behavior (e.g., Stephen, 2013).

This application of evolutionary concepts to psychology is not reliant on the assumption of massive, domain-specific modularity, since predictions derived from such an assumption are often identical to those derived from evolutionary approaches based on plasticity, domain-generality, and cultural evolution. What changes is merely the level on which selection is assumed to act. Whereas a Santa-Barbara school Evolutionary Psychologist would think of selection as acting upon genes coding for domain-specific, yet flexible, mental modules, a more domain-general evolutionary approach would see selection as acting upon the behaviors themselves. In either case, the behaviors and cognitions selected for and against remain the same (Burke, 2014; Stephen, 2014). Indeed, the majority of research in this area does not make direct assumptions about massive modularity or lack thereof (Burke, 2014; Stephen, 2014). The question of whether the mind is massively modular and domain-specific or plastic and culturally selected remains, then, an important empirical question (Barrett et al., 2014), but one that is tangential to the issue of whether evolution offers a useful contribution to the study of mind and behavior (Stephen, 2014).

Irrespective, then, of the unit of selection, we suggest that an evolutionary approach can offer unique insights into understanding and predicting behavior. Indeed, most of the added value brought by an evolutionary approach is reflected in the two neglected aspects (for psychology at least) of Tinbergen's ethological approach to behavior. Evolutionary psychologists are perhaps with good reason shy of admitting that consideration of function may be useful when thinking about behavior. Much of this concern relates to *a posteriori* reasoning, and the criticism of "just so stories." However, a consideration of function *a priori* can be a powerful aid to theorizing and hypothesis generation. In research on disgust, for example, the principal driver behind studying this emotion's relationship with the immune system was based upon the idea that disgust *functions* to aid disease avoidance (Stevenson et al., 2011). Without a consideration of the functional value of this emotion, such avenues of enquiry would not have been envisaged.

A further benefit of an evolutionary approach is in consideration of the phylogenetic origin of a particular behavior. This seems to be a more neglected line of reasoning within human EP, but it can be highly instructive. Again, take disgust as an illustrative example. It has been argued that disgust is a uniquely human emotion, with a small phylogenetic "tail" (Rozin et al., 2010). This "tail" extends into other mammals (and beyond) and has been termed "distaste." Distaste functions primarily as a specific defense against consuming bitter (poisonous) food. However, mammals and indeed all animals face similar pathogen threats to humans, and it would be surprising if we did not also share some of the same basic behaviors to avoid getting sick. In fact, a very extensive set of disease avoidant behaviors have been documented in animals (e.g., Hart, 2011) but surprisingly, almost no research has explored whether the emotion of disgust plays a role in animal disease avoidance. Not only, then, can the idea of phylogenetic continuity act to stimulate new avenues for research, it can also act to complement the functional approach. For example, if animals do use disgust to assist disease avoidance, this would be consistent with the functional interpretation of disgust in humans. Further, Schaller and Murray's (2008) finding of regional personality differences corresponding to pathogen prevalence offers a clear illustration of the use of evolutionary theorizing to generate novel predictions across multiple levels to draw a connection between traditionally disparate domains. Crucially, *none* of this theorizing relies upon a commitment to any particular theory of the unit of selection.

Intra-species color cues may be taken as another example of a *phylogenetic* approach that has advanced our understanding of human behavior. Color is frequently used to convey information in non-human animals. For example, male hooded vultures have highly vascularized, exposed skin on their heads, which flush red during antagonistic encounters, and male ostriches show redder necks during the mating season, suggesting that this hemoglobin-based coloration is a cue to dominance and fertility (Negro et al., 2006). A *phylogenetic* approach allows us to make predictions about the kinds of perceptual biases and behaviors that we expect to see in humans and other species. We know that the majority of mammals have only dichromatic vision that precludes the differentiation of red from green (Carroll et al., 2001), whereas old world, and some new world, primates have trichromatic vision. The *phylogenetic* approach thus allows us to predict that we may see red cues in primates, including humans and old world monkeys, but not in non-primate mammals, and new world monkeys with dichromatic vision (Changizi et al., 2006). This is indeed what we see. The red coloration of mandrills' faces increases with higher position in the dominance hierarchy and with higher testosterone (Setchell and Dixson, 2001). During antagonistic confrontations, the less red male is more likely to back down (Setchell and Wickings, 2005), and female mandrills prefer to mate with redder faced males, irrespective of alpha status (Setchell, 2005). Similarly, in humans, we see redder facial skin in men interpreted as appearing more aggressive, dominant, attractive (Stephen et al., 2012), and healthy (Stephen et al., 2009a,b). Indeed, it has been suggested that one evolved function of trichromatic vision in primates may be to enable individuals to identify color-based social cues (Changizi et al., 2006).

This prediction of human psychological traits based on *phylogenetic* approaches, then, allows enhanced predictive power and greater understanding of the psychology of humans.

e-COGNITION'S PROXIMAL EXPLANATORY NATURE

Barrett et al. (2014) suggest that an alternative to the standard computational theories of mind (in which they include Santa Barbara school EP) is the various e-cognition approaches. They focus on one form, the extended mind hypothesis (e.g., Clark and Chalmers, 1998), which holds that the boundaries of cognition extend well beyond the central nervous system, so that the body and the environment form a coupled system that governs behavior. The main benefit of such an approach, according to Barrett et al. (2014), is that it encompasses the complex array of external features (e.g., written language, visual aids, etc.) that shape human behavior in the current environment.

While we agree that e-cognition approaches offer potentially interesting ways of understanding behavior, we would also argue that they are essentially elaborations of the computational models of mind that Barrett et al. (2014) criticize, representing extensions of Tinbergen's (1963) *causal* (mechanistic), and *ontogenetic* (developmental) levels of explanation. Extending the boundary of cognition to include objects that are not typically considered as part of the cognitive system (e.g., a shopping-list memory aid) does not address a *functional* or *phylogenetic* level of analysis, any more than does a standard computational approach. This can only be achieved by studying behavior through the evolutionary concepts of selection and fitness. As such, Barrett et al.'s suggested alternative to EP—e-cognition—does not represent a true alternative to computational models of mind, but rather an extension of these approaches that should be best approached through the lens of evolutionary theory. In this way, Barrett et al.'s (2014) conception of e-cognition as an alternative to evolutionary approaches to cognition and behavior mischaracterizes e-cognition as an ultimate explanatory framework, when it should properly be considered proximal (see Scott-Phillips et al., 2011, for similar arguments in response to previously proposed alternative ultimate explanatory frameworks, such as cultural evolution and epigenetics).

CONCLUSIONS

Accordingly, we argue that evolutionary approaches provide significant additional predictive and explanatory value above standard computational models by allowing researchers to address the *phylogenetic* and *functional* levels of explanation. Evolutionary approaches to mind and behavior, then, go well beyond existing approaches in their potential to provide an understanding, not necessarily of the how, but of the why, humans behave as they do in an unpredictable world. Consider, for example, the richness and complexity of human emotion: forged over the course of human evolution and responding to present day triggers, the passions drive behavior—albeit often to dysfunctional ends within modern societies (e.g., Fitness and Case, 2003). Understanding such diverse emotions as anger, jealousy, hate, love, disgust, or shame as evolution's executioners (Wright, 1995) provides us with an answer to the question of the "why" of behavior that cannot be addressed by only *causal* and *ontogenetic* levels of analysis. In short, e-cognition accounts, along with other approaches that do not hold the evolutionary principles of selection and fitness as central represent only extensions of the more proximate explanations of mind and behavior, rather than providing the fuller understanding of cognition and behavior that ensues from *phylogenetic* and *functional* level of explanations. Further, one extraordinary achievement of evolutionary approaches to mind and behavior has been to demonstrate the commonalities shared by human beings across time and space as a function of the adaptive problems they have always faced, and continue to face, as social animals who depend upon one another for their survival. Certainly, humans today are confronted with a material, technological world that could not be imagined by humans who lived thousands of years ago. However, a baby from our recent evolutionary past miraculously transported through time to a modern Western environment would still crave attachment and belonging, experience, and respond to the world and others through her senses and feelings, and learn through language how to interpret, communicate, and function more or less adaptively in that environment, just as babies raised in regions geographically distant from their ancestral homelands do today. No doubt she would also help her parents program their latest iPhone along the way.

REFERENCES

Barrett, L., Pollet, T., and Stulp, G. (2014). From computers to cultivation: reconceptualising evolutionary psychology. *Front. Psychol.* 5:867. doi: 10.3389/fpsyg.2014.00867

Burke, D. (2014). Why isn't everyone an evolutionary psychologist? *Front. Psychol.* 5:910. doi: 10.3389/fpsyg.2014.00910

Carroll, J., Murphy, C. J., Neitz, M., Ver Hoeve, J. N., and Neitz, J. (2001). Photopigment basis for dichromatic color vision in the horse. *J. Vis.* 1, 80–87. doi: 10.1167/1.2.2

Changizi, M. A., Zhang, Q., and Shimojo, S. (2006). Bare skin, blood and the evolution of primate colour vision. *Biol. Lett.* 2, 217–221. doi: 10.1098/rsbl.2006.0440

Clark, A., and Chalmers, D. J. (1998). The extended mind. *Analysis* 58, 7–19. doi: 10.1093/analys/58.1.7

Cosmides, L., and Tooby, J. (1987). "From evolution to behaviour: evolutionary psychology as the missing link," in *The Latest on the Best: Essays on Evolution and Optimality*, ed J. Dupre (Cambridge, MA: The MIT Press), 277–306.

Fitness, J., and Case, T. I. (2003). Commentary on "the evolution of the social mind": The emotional brain drives the social mind. *Connexions* 6, 17–20. Available online at: http://www.open.ac.uk/Arts/connex/issue6-contents.htm

Hart, B. (2011). Behavioural defences in animals against pathogens and parasites: parallels with the pillars of medicine in humans. *Philos. Trans. R. Soc. Lond.* 366B, 3406–3418. doi: 10.1098/rstb.2011.0092

Laland, K., and Brown, G. (2011). *Sense and Nonsense: Evolutionary Perspectives on Human Behaviour, 2nd Edn.*, Oxford: Oxford University Press.

Negro, J. J., Sarasola, J. H., Farinas, F., and Zorrilla, I. (2006). Function and occurrence of facial flushing in birds. *Comp. Biochem. Physiol. A* 143, 78–84. doi: 10.1016/j.cbpa.2005.10.028

O'Brien, D. T., and Gallup, A. C. (2011). Using Tinbergen's four questions (plus one) to facilitate evolution education for human-oriented disciplines. *Evol. Educ. Outreach* 4, 107–113. doi: 10.1007/s12052-010-0305-2

Rozin, P., Haidt, J., and McCauley, C. (2010). "Disgust," in *Handbook of Emotions*, eds M. Lewis, J. Haviland, and L. Barrett (New York, NY: Guilford Press), 757–776.

Schaller, M., and Murray, D. R. (2008). Pathogens, personality and culture: disease prevalence predicts worldwide variability in sociosexuality, extraversion, and openness to experience. *J. Pers. Soc. Psychol.* 95, 212–221. doi: 10.1037/0022-3514.95.1.212

Scott-Phillips, T. C., Dickins, T. E., and West, S. A. (2011). Evolutionary theory and the ultimate-proximate distinction in human behavioural sciences. *Perspect. Psychol. Sci.* 6, 38–47. doi: 10.1177/1745691610393528

Setchell, J. M. (2005). Do female mandrills prefer brightly colored males? *Int. J. Primatol.* 26, 715–735. doi: 10.1007/s10764-005-5305-7

Setchell, J. M., and Dixson, A. F. (2001). Changes in the secondary sexual adornments of male mandrills (*Mandrillus sphinx*) are associated with gain and loss of alpha status. *Horm. Behav.* 39, 177–184. doi: 10.1006/hbeh.2000.1628

Setchell, J. M., and Wickings, E. J. (2005). Dominance, status signals and coloration in male mandrills (*Mandrillus sphinx*). *Ethology* 111, 25–50. doi: 10.1111/j.1439-0310.2004.01054.x

Stephen, I. D. (2013). On aims and methods of facial attractiveness research: The lasting influence of Tinbergen (1963). *Hum. Ethol. Bull.* 28, 31–38. Available online at: http://media.anthro.univie.ac.at/ishe_journal/index.php/heb/article/view/101/69

Stephen, I. D. (2014). Putting the theory before the data: is "massive modularity" a necessary foundation of evolutionary psychology? *Front. Psychol.* 5:1158. doi: 10.3389/fpsyg.2014.01158

Stephen, I. D., Coetzee, V., Law Smith, M., and Perrett, D. I. (2009a). Skin blood perfusion and oxygenation colour affect perceived human health. *PLoS ONE* 4:e5083. doi: 10.1371/journal.pone.0005083

Stephen, I. D., Law Smith, M. J., Stirrat, M. R., and Perrett, D. I. (2009b). Facial skin coloration affects perceived health of human faces. *Int. J. Primatol.* 30, 845–857. doi: 10.1007/s10764-009-9380-z

Stephen, I. D., Oldham, F. H., Perrett, D. I., Barton, R. A. (2012). Redness enhances perceived aggression, dominance and attractiveness in men's faces. *Evol. Psychol.* 10, 562–572. Available online at: http://www.epjournal.net/articles/redness-enhances-perceived-aggression-dominance-and-attractiveness-in-mens-faces/

Stevenson, R. J., Hodgson, D., Oaten, M., Barouei, J., and Case, T. I. (2011). The effect of disgust on oral immune function. *Psychophysiology* 48, 900–907. doi: 10.1111/j.1469-8986.2010.01165.x

Tinbergen, N. (1963). On aims and methods of ethology. *Anim. Biol.* 55, 297–321. doi: 10.1163/157075605774840941

Wright, R. (1995). *The Moral Animal: Evolutionary Psychology and Everyday Life.* New York, NY: Vintage Books.

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 07 October 2014; accepted: 11 November 2014; published online: 28 November 2014.

Citation: Stephen ID, Mahmut MK, Case TI, Fitness J and Stevenson RJ (2014) The uniquely predictive power of evolutionary approaches to mind and behavior. Front. Psychol. 5:1372. doi: 10.3389/fpsyg.2014.01372

This article was submitted to Evolutionary Psychology and Neuroscience, a section of the journal Frontiers in Psychology.

frontiers in Psychology

OPINION
published: 21 April 2015
doi: 10.3389/fpsyg.2015.00419

The not-always-uniquely-predictive power of an evolutionary approach to understanding our not-so-computational nature

Gert Stulp[1]*, *Thomas V. Pollet*[2] *and Louise Barrett*[3]

[1] *Department of Population Health, London School of Hygiene & Tropical Medicine, London, UK,* [2] *Department of Social and Organizational Psychology, VU University Amsterdam, Amsterdam, Netherlands,* [3] *Department of Psychology, University of Lethbridge, Lethbridge, AB, Canada*

Keywords: evolutionary psychology, cognition, cognitive integration, modules, extended mind

Edited by:
Danielle Sulikowski,
Charles Sturt University, Australia

Reviewed by:
Darren Burke,
University of Newcastle, Australia

***Correspondence:**
Gert Stulp,
gert.stulp@lshtm.ac.uk

Specialty section:
This article was submitted to Evolutionary Psychology and Neuroscience, a section of the journal Frontiers in Psychology

Received: *17 February 2015*
Accepted: *25 March 2015*
Published: *21 April 2015*

Citation:
Stulp G, Pollet TV and Barrett L (2015) The not-always-uniquely-predictive power of an evolutionary approach to understanding our not-so-computational nature. Front. Psychol. 6:419. doi: 10.3389/fpsyg.2015.00419

Introduction

We thank Klasios (2014)[1] and Stephen et al. (2014)[2] for their commentaries on our paper (Barrett et al., 2014)[3]. Criticisms like these can only help to improve the quality of arguments offered on both sides. Both Klasios's and Stephen et al.'s commentaries generate misconceptions, however, about the aim of our article and our stated position. Before we respond more generally to their arguments, we want to correct these mistaken impressions.

First, Klasios states that we misinterpret the EP notion of computation. This is simply false. We do not argue that EP posits a physical architecture. Our characterization of the EP view (p. 3) is that it "relies heavily on analogies to computational algorithms, functions, inputs, and outputs" and that its research strategy "involves . . . hypothesizing the kinds of algorithmic "design features" that any psychological adaptation would require in order to solve such a problem." The notion of a physical architecture was raised in response to Robert Kurzban's implied suggestion that psychological adaptations are analogous to morphological (i.e., physical) adaptations, and can be reverse engineered in the same way. We disputed Kurzban's argument precisely because there are no grounds for positing a particular kind of physical architecture that could serve to support such an analogy (see also Peters, 2013).

Second, Stephen et al. (2014) present our argument as stating that the primary contribution of an evolutionary approach to psychology is the idea of massive modularity when, in fact, we stated merely that the modularity of evolved adaptations is the primary *distinction* between EP and standard computational theories. We do not consider modularity to be the primary contribution of an evolutionary approach to human behavior, as should be clear from our previous work (e.g., Barrett et al., 2001; Pollet et al., 2009; Stulp and Barrett, 2014), as well as our argument in the original paper.

Both these misconceptions perhaps arise because of a failure to appreciate that we were addressing the specific question posed for this research topic: is EP the obvious alternative to standard computational approaches to the mind? Our answer was that one evolutionary approach to psychology (i.e., the "Santa Barbara School" of Evolutionary Psychology, which we refer to as EP throughout this piece) was not an alternative approach, nor could it be,

---

[1] http://journal.frontiersin.org/article/10.3389/fpsyg.2014.01348/full
[2] http://journal.frontiersin.org/article/10.3389/fpsyg.2014.01372/full
[3] http://journal.frontiersin.org/article/10.3389/fpsyg.2014.00867/full

precisely because it *is* a computational theory. As such, it could only be distinguished from other cognitive approaches via the manner in which it applied evolutionary thinking. A large part of our paper was then devoted to why we felt the particular evolutionary approach adopted—namely, modular psychological adaptation—fell short. Other evolutionary approaches are not vulnerable to this criticism, and so we did not include these in our analysis. Thus, nowhere do we dispute Stephen et al.'s main point that evolutionary theory is useful for explaining human behavior and that, using Tinbergen's integrative approach, one can generate unique predictions (see also Barrett and Stulp, 2013).

The Not-Always-so-Uniquely Predictive Ability of Evolutionary Theory

We do want to add, however, that evolutionary theory may not always be as uniquely predictive as Stephen et al.'s examples suggest. With respect to disgust, we read (p. 2): "the principal driver behind studying this emotion's relationship with the immune system was based upon the idea that disgust functions to aid disease avoidance (Stevenson et al., 2011)" and that such "avenues of enquiry would not have been envisaged" without evolutionary theorizing. Their confidence in the latter statement is perhaps misplaced, however, as Stevenson et al.'s (2011) research drew explicitly on earlier findings by Bosch et al. (2001) that were obtained without any reference to either disgust or evolutionary theory (as acknowledged by Stevenson et al., p. 900). At best, then, we might say that, in this case, the functional explanation represents a plausible *post-hoc* account and further clarification of an already established phenomenon, rather than that the functional perspective made unique predictions that allowed the phenomenon to be identified in the first place.

Similarly, in their second example, Stephen et al. predict that species with trichromatic vision (i.e., the ability to distinguish red from green) will make use of red coloration as cues and signals more than dichromats. Again, the prediction that animals unable to see red will not make use of red coloration, whereas those animals that can see red potentially might do so, is in itself not a very strong evolutionary prediction, given that one could just as easily formulate such a prediction solely on an understanding of extant species' visual systems. It is, however, important to note that we are not denying the importance of evolutionary theory. Our point is simply that we should not overstate its power to generate unique predictions and empirical findings that would otherwise not occur. Similarly, most findings in evolutionary psychology are, as the authors of many of these articles themselves note, consistent with evolutionary predictions, but do not rule out other potential explanations.

Ultimately Proximate?

Stephen et al.'s second point is that we have confused proximate and ultimate levels of explanation. Specifically, they state that "Barrett et al.'s (2014) conception of e-cognition as an alternative to evolutionary approaches to cognition and behavior mischaracterizes e-cognition as an ultimate explanatory framework, when it should properly be considered proximal" (p. 2). We believe this criticism is unwarranted for several reasons. First, we raised E-cognition as an alternative to the standard cognitivist, computational approach to psychology, and *not* to a functional evolutionary approach. We do not dispute that phylogenetic and functional levels of explanation can provide additional "explanatory value above standard computation models" (p. 3). Our actual argument was that E-cognition, and cognitive integration in particular, could fill some of the gaps left open by current information-processing approaches, and we said nothing to suggest that this should occur to the exclusion of evolutionary theory. Rather, our point was that, to take Stephen et al.'s example, seeking answers to how and why humans can program things like iPhones (and obviously conceive of and manufacture them in the first place) seems crucial to achieving a "fuller understanding of cognition and behavior" (p. 3) than we currently possess. Stephen et al. must surely agree that such a full understanding goes well beyond the phylogenetic and functional levels of explanation, and our closing plea for explanatory pluralism was made precisely for this reason. Klasios, while (surprisingly) using this point against us, actually agrees on this when he states that "[a]t a pragmatic level, different research programs will simply find it profitable to have differing explanatory focuses and emphases" (p. 1).

Second, nowhere did we "mischaracterize" E-cognition as an ultimate framework, in just the same way that no one argues that information-processing theories represent an ultimate framework. Both are guiding theories that take a particular stance on the nature of cognitive processes and, in that sense, both can be seen as more proximate than ultimate. Some E-cognition theories may stand on their own without referring to evolutionary theory, in the same way that most information-processing-theories similarly lack this explicit connection. That said, Stephen et al. perhaps jumped the gun by stating that E-cognition is a proximate and not an ultimate approach, without providing any reason as to why this is the case. Indeed, some forms of E-cognition are fundamentally evolutionary. For instance, certain aspects of the extended mind argument have been made in an explicitly evolutionary way, captured by Clark's (2005) "007 Principle" and Rowlands' (2003) "barking dog principle." Both of these suggest that a thrifty evolutionary process will not build internal resources (especially expensive neural tissue) if the structure of the environment itself can be exploited in a way that can bear some of the cognitive burden. Distributed, extended cognition is thus the process by which internal resources are replaced or complemented by reliable external structures, with the idea that organisms that pursue this route will achieve higher fitness. This is supported by analogies from other species (for example, the manner in which the physics of a cricket's body automatically filters out extraneous sounds; a process that would otherwise need to be performed by neural tissue: Barrett, 2011) and so the extended mind also adopts the phylogenetic perspective for which Stephen et al. advocate.

Openness to Change Rather than Constancy as a Constant

Klasios, in contrast, believes that our suggestion for E-cognition as an alternative to standard computational approaches stems from our flawed understanding of computation, and that "there is nothing within the theoretical approach of evolutionary psychology that in principle denies the existence of … 'E-cognition'" (p. 1). We disagree strongly with this point, and tackle it in conjunction with Klasios's assessment that "our discussion of human nature is also problematic" (p. 1). The latter assertion seems to be based on a misreading of Wheeler and Clark (2008) statement that our extended cognitive architecture's "constancy lies mainly in *its continual openness to change*" (p. 3572, emphasis added). While we take "change" to be the key here, Klasios takes it to be "constancy," arguing that EP recognizes "this underlying constancy and refers to it as our underlying 'developmental programs'" (p. 1). Klasios' apparent misunderstanding of Wheeler and Clark's position leads nicely into a consideration the fundamental differences between E-cognition and computational theories.

It is important to note that we completely agree that some varieties of E-cognition can be seen as complementary to computational theories, given that they raise no objections to a rules-and-representations approach (as we explicitly addressed in our paper; p. 10). The EP position on psychological phenomena as adaptations, however, does not, in fact, gel very well with E-cognition, since the latter argues for the deep intertwining of brain, body and environment, whereas EP emphasizes a disjunction between these elements. EP's premise is that cognitive processes occur in the brain alone, and that our psychology is adapted to a past (environment) that in large part no longer exists, hence we are often mismatched to the modern world (e.g., Tooby and Cosmides, 1990). In this view, our psychological processes may often operate in opposition to the world around us, whereas the E-cognition view is that body and environment should be considered as integral parts of the cognitive system. We can see this even more clearly in Klasios's suggestion that EP deals only with a functional level of explanation that "abstracts away from instantiations in brain, body and the larger context in which they are embedded" (p. 1). In addition to the fact that the concept of an "abstracted adaptation" is entirely unclear to us, this position is fundamentally at odds with an E-cognition view which holds that no such abstraction is possible because cognitive processes are precisely a function of a brain embedded in a body embedded in an environment, all of which make crucial, often constitutive, contributions to those cognitive processes (e.g., Clark, 1997).

Klasios goes on to suggest that we misrepresent the EP view on human nature by neglecting Sperber's notion of epidemiological culture (see e.g., Sperber, 1996), which, according to Klasios, is equivalent to an E-cognition approach. Sperber's (1996) argument is, however, focused more strongly on how existing (evolved) psychological structures influence the kinds of cultural patterns produced (as captured in his notion of "cultural attractors"), with less emphasis placed on how culture actively alters our psychology. This is perhaps to be expected given that Sperber (1996) adheres to a standard EP view of psychological adaptations (modules) to past environments (also note that epidemiological or transmitted culture is given far less prominence in Tooby and Cosmides' conception of culture than Klasios suggests). Sperber's more recent position is that cultural phenomena "invade and inflate" our evolved mental modules, often resulting in "mismatches" between evolved function and current usage (Sperber and Hirschfeld, 2004), whereas cognitive integration argues that our psychology is never fixed but continually transformed as it incorporates various kinds of cultural artifacts (including the iPhone).

Conclusion

Again, we would like to thank John Klasios and Ian Stephen and colleagues for engaging in this discussion and providing us with the opportunity to clarify our position. We hope our original paper and this reply continue to spark debate on our computational nature or lack thereof.

References

Barrett, L. (2011). *Beyond the Brain: How Body and Environment Shape Animal and Human Minds*. New Jersey, NJ: Princeton University Press.

Barrett, L., Dunbar, R. I. M., and Lycett, J. (2001). *Human Evolutionary Psychology*. Basingstoke: Palgrave.

Barrett, L., Pollet, T. V., and Stulp, G. (2014). From computers to cultivation: reconceptualizing evolutionary psychology. *Front. Psychol.* 5:867. doi: 10.3389/fpsyg.2014.00867

Barrett, L., and Stulp, G. (2013). Four more reasons why ethology matters: tinbergen and the human sciences. *Hum. Ethol. Bull.* 28, 39–49.

Bosch, J. A., de Geus, E. J., Kelder, A., Veerman, E. C., Hoogstraten, J., and Amerongen, A. V. (2001). Differential effects of active versus passive coping on secretory immunity. *Psychophysiology* 38, 836–846. doi: 10.1111/1469-8986.3850836

Clark, A. (1997). *Being there: Putting Brain, Body, and World Together Again*. Cambridge, MA: MIT press.

Clark, A. (2005). Beyond the flesh: some lessons from a mole cricket. *Artif. Life* 11, 233–244. doi: 10.1162/1064546053279008

Klasios, J. (2014). Our computational nature: comment on Barrett et al. *Front. Psychol.* 5:1348. doi: 10.3389/fpsyg.2014.01348

Peters, B. M. (2013). Evolutionary psychology: neglecting neurobiology in defining the mind. *Theory Psychol.* 23, 305–322. doi: 10.1177/0959354313480269

Pollet, T. V., Fawcett, T. W., Buunk, A. P., and Nettle, D. (2009). Sex-ratio biasing towards daughters among lower-ranking co-wives in Rwanda. *Biol. Lett.* 5, 765–768. doi: 10.1098/rsbl.2009.0394

Rowlands, M. (2003). *Externalism: Putting Mind and World Back Together Again*. Montreal, QC: McGill-Queen's Press.

Sperber, D. (1996). *Explaining Culture—A Naturalistic Approach*. Oxford: Blackwell Publishers Ltd.

Sperber, D., and Hirschfeld, L. A. (2004). The cognitive foundations of cultural stability and diversity. *Trends Cogn. Sci.* 8, 40–46. doi: 10.1016/j.tics.2003.11.002

Stephen, I. D., Mahmut, M. K., Case, T. I., Fitness, J., and Stevenson, R. J. (2014). The uniquely predictive power of evolutionary approaches to mind and behavior. *Front. Psychol.* 5:1372. doi: 10.3389/fpsyg.2014.01372

Stevenson, R. J., Hodgson, D., Oaten, M. J., Barouei, J., and Case, T. I. (2011). The effect of disgust on oral immune function. *Psychophysiology* 48, 900–907. doi: 10.1111/j.1469-8986.2010.01165.x

Stulp, G., and Barrett, L. (2014). Evolutionary perspectives on human height variation. *Biol. Rev. Camb. Philos. Soc.* doi: 10.1111/brv.12165. [Epub ahead of print]

Tooby, J., and Cosmides, L. (1990). The past explains the present: emotional adaptations and the structure of ancestral environments. *Ethol. Sociobiol.* 11, 375–424. doi: 10.1016/0162-3095(90)90017-Z

Wheeler, M., and Clark, A. (2008). Culture, embodiment and genes: unravelling the triple helix. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 363, 3563–3575. doi: 10.1098/rstb.2008.0135

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Psychology

GENERAL COMMENTARY
published: 22 April 2015
doi: 10.3389/fpsyg.2015.00498

Evolved computers with culture. Commentary: From computers to cultivation: reconceptualizing evolutionary psychology

Gregory A. Bryant *

Department of Communication, University of California, Los Angeles, Los Angeles, CA, USA

Keywords: computational theory of mind, domain specificity, evolutionary psychology, cultural learning, e-cognition

A commentary on

From computers to cultivation: reconceptualising evolutionary psychology
by Barrett, L., Pollet, T., and Stulp, G. (2014). Front. Psychol. 5:867. doi: 10.3389/fpsyg.2014.00867

Barrett et al. review recent developments in evolutionary psychology (EP) and conclude that EP offers little in way of theoretical advancement over standard computational theory of mind (CTM) accounts, because traditional approaches in psychology implicitly accept that cognition is evolved. To Barrett et al., historical resistance to EP is surprising given that EP assumes the traditional computational-representational model of cognition. Across cognitive psychology, however, evolutionary approaches are sometimes accepted, but often mostly ignored. Vision and auditory perception researchers are typically functionalist, and as a result have made advances exceeding other areas of cognitive science—these scholars are often friendly to EP at least in some form. But many other areas have neither adopted a functionalist perspective nor currently accept the research program of EP. Certainly, most researchers in cognitive psychology do not attempt to reverse engineer computational solutions to adaptive problems as EP does. Not coincidentally, many cognitive psychologists study what EP would consider nonfunctional by products.

Still, it is true that EP has largely embraced cognitive psychology (though actual cognitive research is still surprisingly rare) and has integrated it with theories from evolutionary biology. Barrett et al. suggest that the adoption of the CTM constitutes a weakness for EP and they instead propose that various forms of e-cognition (i.e., embodied, embedded, enactive) offer a viable alternative to computational approaches. But as Klasios (2014) pointed out in his recent commentary, Barrett et al. fail to recognize that "cognitive integration" is information processing, and in its most basic sense, is necessarily computational. As Gallistel and King (2009) recently put it, describing the mind as a case of digital computation "is the only game in town" (p. 24). There is no scientific alternative to the notion that the neural coding of events in the world involves the probabilistic transformation of information. If one admits that much, logical entailments prevent the kind of rejection of the CTM that Barrett et al. endorse.

Notions of e-cognition can be provocative, and on the surface can seem like an advancement in our ideas about human cognition. However, there are some fundamental problems in the current presentation and the ideas in general. By suggesting that our cognition is shaped by cultural artifact use, I believe Barrett et al. point the causal arrow mostly backwards. That is not to say that artifacts cannot, in principle, affect brain organization, but the evidence to date seems to favor the idea that cultural phenomena are generally tailored to our brains and bodies, not the reverse (Claidiere and Sperber, 2007). For instance, the authors use the example of time-pieces contributing to culturally

OPEN ACCESS

Edited by:
Danielle Sulikowski,
Charles Sturt University, Australia

Reviewed by:
Thom Scott-Phillips,
Durham University, UK

****Correspondence:***
Gregory A. Bryant,
gabryant@ucla.edu

Specialty section:
This article was submitted to Evolutionary Psychology and Neuroscience, a section of the journal Frontiers in Psychology

Received: *23 March 2015*
Accepted: *08 April 2015*
Published: *22 April 2015*

Citation:
Bryant GA (2015) Evolved computers with culture. Commentary: From computers to cultivation: reconceptualizing evolutionary psychology. Front. Psychol. 6:498. doi: 10.3389/fpsyg.2015.00498

evolved values associated with timeliness, and they attribute timeliness as being part of our human nature, essentially arguing that extended artifacts like time-pieces have altered our cultural cognitive machinery. There is no question that inventions like time-pieces feed back into practices and beliefs—the more we advance the technology, the more we allow ourselves to be manipulated by it. But timeliness is a byproduct of social coordination, cooperation, and reciprocity. If an individual demands that her associate pay attention to the time—an ability afforded by a time-piece—and then the associate does not abide when able to do so, he is implicitly discounting the value of the relationship. The human nature component in this example is not the timeliness per se, but the use of culturally evolved norms as a means to coordinate social interactions.

Admittedly, the ways neural coding schemes relate to various phenomena in the world, external to the brain itself, constitute hard empirical questions that will almost certainly need to incorporate many complexities suggested by various forms of e-cognition. These issues will likely be resolved, however, within a framework that involves, at its theoretical core, computational mechanisms implemented in the brain. Even if some of the external phenomena that e-cognition proponents describe constituted legitimate examples of extended phenotypic traits (Dawkins, 1982), their implementation would still land squarely in the neural circuitry of the brain interfacing with motor systems. For example, written language is learned by people quite effectively and writing systems are shaped by both cultural and cognitive factors, including visual processing and memory systems. There is evidence of a brain area that, when given certain input, reliably develops expertise for visual words (Dehaene, 2009), showing amazing flexibility in how brain structure interacts with culture (Barrett, 2012). But our understanding of the psychology of reading is purely computational. Similarly, we don't need a special theory of beaver cognition because of beaver dams—we just need to explain the evolved cognitive and behavioral processes that allow beavers to build them.

Evolutionary behavioral scientists who study culture often rely on the concept of domain generality, presumably because cultural phenomena seemingly incorporate so many aspects of our cognition and environment. Of course, culture is deeply interconnected with many facets of our cognitive processing, but that does not require a system that is infinitely flexible and unconstrained by past selection. Rather, culture is rooted in a suite of cognitive and communicative abilities that allow us to transmit rich information vertically and horizontally, and the outputs of such processes feedback iteratively into an evolutionarily dynamic cultural knowledge system rooted in adaptive computational design. Cultural transmission often follows certain patterns resulting in stable psychological and communicative strategies that have all the hallmarks of domain specificity: (i) our attention is directed in specific ways to particular relevant agents, (ii) motivational systems drive the spreading of specific kinds of information, and iii) cultural learning systems are content sensitive.

The authors acknowledge the idea that there is no defensible dividing line between domain specific and domain general mechanisms (Barrett and Kurzban, 2006), but then they fail to properly appreciate this in their treatment of certain culturally learned information, such as the special status of incest taboos in cultural transmission. In the example given, Barrett et al. fail to acknowledge the possibility that unconscious processes guiding incest avoidance (Lieberman et al., 2007) were driving the mating decisions described by Durham (2002) despite variations over time in the local cultural rules. Overall, they emphasize examples of domain-general mechanisms potentially solving problems that some evolutionary psychologists consider only manageable by highly specialized domain-specific systems—but seem to momentarily forget that just because a mechanism works across content domains, it is still functionally specialized. The scope of a mechanism is independent from whether it has design features (i.e., functional specialization) (Barrett and Kurzban, 2006). Cognitive mechanisms, including associative learning processes and various decision making systems sensitive to local information, can operate on representations across multiple domains and subsequently feed into more specialized systems—cognition is hierarchically structured, and evolutionarily conserved (Barrett, 2012). So where is the argument exactly?

Despite these disagreements—some apparent, some real—Barrett et al. seem to illustrate that the historical gap between behavioral ecology and evolutionary psychology is closing, not widening. Many evolutionary psychologists are developing a greater appreciation for cultural evolution and behavioral flexibility, and behavioral ecologists are more concerned now with cognitive adaptations and experimental psychology methodology. Both fields have led the behavioral sciences in cross-cultural fieldwork, and to a great extent, we share a theoretical foundation. Don Symons's question (1987) still looms, however: If we're all Darwinians, what's the fuss about?

References

Barrett, H. C. (2012). A hierarchical model of the evolution of human brain specializations. *Proc. Natl. Acad. Sci. U.S.A.* 109(Suppl. 1), 10733–10740. doi: 10.1073/pnas.1201898109

Barrett, H. C., and Kurzban, R. (2006). Modularity in cognition: framing the debate. *Psychol. Rev.* 113, 628–647. doi: 10.1037/0033-295X.113.3.628

Claidiere, N., and Sperber, D. (2007). The role of attraction in cultural evolution. *J. Cogn. Cult.* 7, 89–111. doi: 10.1163/156853707X171829

Dawkins, R. (1982). *The Extended Phenotype*. Oxford: WH Freeman.

Dehaene, S. (2009). *Reading in the Brain*. New York, NY: Viking.

Durham, W. H. (2002). "Cultural variation in time and space: the case for a populational theory of culture," in *Anthropology Beyond Culture*, eds R. G. Fox and B. J. King (Oxford: Berg), 193–206.

Gallistel, C. R., and King, A. P. (2009). "Information," in *Memory and the Computational Brain: Why Cognitive Science Will Transform Neuroscience* (Oxford: Wiley-Blackwell). doi: 10.1002/9781444310498.ch1

Klasios, J. (2014). Our computational nature: comment on Barrett et al. *Front. Psychol.* 5:1348. doi: 10.3389/fpsyg.2014.01348

Lieberman, D., Tooby, J., and Cosmides, L. (2007). The architecture of human kin detection. *Nature* 445, 727–731. doi: 10.1038/nature05510

Symons, D. (1987). "If we're all Darwinians, what's the fuss about?" in *Sociobiology and Psychology*, eds C. B. Crawford, M. F. Smith, and D. L. Krebs (Hillsdale, NJ: Erlbaum), 121–146.

Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in Psychology

OPINION
published: 22 July 2015
doi: 10.3389/fpsyg.2015.01047

Evolved biocultural beings (who invented computers)

Louise Barrett[1]*, **Thomas V. Pollet**[2] **and Gert Stulp**[3]

[1] Department of Psychology, University of Lethbridge, Lethbridge, AB, Canada, [2] Department of Social and Organizational Psychology, VU University Amsterdam, Amsterdam, Netherlands, [3] Department of Population Health, London School of Hygiene and Tropical Medicine, London, UK

Keywords: evolutionary psychology, extended mind, cognition, culture, embodied cognition

Introduction

Many thanks to Bryant (2015) for keeping the conversation lively, and engaging in further debate on our paper (Barrett et al., 2014). Although Bryant raises several interesting points, it appears that, as with our previous commentators, there was some misunderstanding of our aim, which simply was to answer the question posed for us: does evolutionary psychology represent an alternative to computational theories of mind? To reiterate, we suggested that Santa Barbara-style EP could not be an alternative given that it already is a computational theory of mind. Bryant (2015) apparently considers this question ill-posed, given his assertion that viewing "the mind as a case of digital computation" is "the only game in town." Our friendly suggestion here is that perhaps he needs to get out a little more, and sample more fully the alternatives on offer.

OPEN ACCESS

Edited by:
Danielle Sulikowski,
Charles Sturt University, Australia

Reviewed by:
Michael Stirrat,
University of Stirling, UK

***Correspondence:**
Louise Barrett,
louise.barrett@uleth.ca

Specialty section:
This article was submitted to
Evolutionary Psychology and
Neuroscience,
a section of the journal
Frontiers in Psychology

Received: 29 April 2015
Accepted: 09 July 2015
Published: 22 July 2015

Citation:
Barrett L, Pollet TV and Stulp G (2015)
Evolved biocultural beings (who
invented computers).
Front. Psychol. 6:1047.
doi: 10.3389/fpsyg.2015.01047

Not the Only Metaphor in Town

> "Freud often compared the brain to hydraulic and electro-magnetic systems. Leibniz compared it to a mill, and I am told the ancient Greeks thought the brain functions like a catapult. At present, obviously, the metaphor is the digital computer."
> ∼ John Searle

To assert that there is no alternative to digital computation is a philosophically weak position, not least because the history of science provides ample evidence of prominent ideas eventually shown to be wrong: phlogiston and the luminiferous aether were also "the only game in town" once upon a time. The brain has been likened to many other cultural tools that were, unsurprisingly, considered to be of great significance in their time; the computational metaphor is one in a long line of metaphors that reflect the most advanced technology of their day. There is no reason to imagine that we have finally managed to hit on the correct one, as opposed to the one that just reflects something about the times in which we live (Barrett, 2011).

Our main point, though, is that digital computation really isn't the only game in town. Among other work cited in our original paper, Chemero (2009) provides the most recent and comprehensive treatment of a non-computational-representational approach to mind (see also Anderson (2014, 2015) for a more neuroscientifically-focused account that similarly concludes the best way to understand the brain may be in enactive and ecological terms). Furthermore, this approach is not restricted to philosophical theorizing but also includes empirical work (see Dotov et al., 2010, as well as the examples given in Chemero, 2009). There have also been earlier incarnations of a non-representational approach to cognition (e.g., Rosch et al., 1992; Thelen and Smith, 1994; Kelso, 1997) along with Gibson's (1979) anti-representational theory of perception (see Barrett, 2011 for a review). Given Bryant's (2015) assertion of no scientific alternative to computation, he implies either that such genuinely non-computational-representational approaches do not qualify as science, or else he has misunderstood them. Although all we need do to counter Bryant's position is point to these scientifically credible alternatives, in what follows we consider briefly some of the arguments against a strong computational position. We then go on to discuss his other assertions regarding the relationship between culture and cognition.

It is telling that Bryant (2015) adopts a rather "Hegelian" approach in his commentary (see Chemero, 2009, and our original article), asserting the necessity of digital computation and information processing (conceived in terms of Shannon information theory: G. Bryant, Pers. Comm.), rather than providing arguments or evidence for it. As Wallace (2007) discusses, echoing Searle (1990) before him, the notion of the brain as engaged in digital computation is not a scientific discovery, like the moons of Saturn, but is instead a claim: a claim that looking at the brain in this particular way is useful. As Wallace (2007) argues, Shannon's theory was a pragmatic solution to an explicitly human engineering problem, and was never intended as a scientific theory of cognition. Using Shannon information to model human cognition is fundamentally flawed because, as Wallace (2007) discusses, human cognitive systems violate the assumptions under which Shannon information applies. Wallace (2007) further notes that use of terms like "information processing" to describe brain function can lead to a dualist position. Such thinking pervades Klasios's (2014) commentary, for example, when he argues that EP deals only with information processing and not neural activity as such, giving rise to the brain possessing two distinct qualities: the material activity of its neurons and, as Wallace (2007) calls it, the non-material, "mysterious world of information."

Bryant's argument rests on the notion that adopting an information theoretic view is, in essence, a functionalist perspective, asking what role a given process plays, rather than the specific manner in which it is brought about or implemented. This is entirely reasonable—such a position has helped avoid a particular kind of "neural chauvinism" that suggests there is something inherently special about biological brains, so excluding any form of artificial intelligence from consideration. In addition, cognitive integration is often characterized as a form of "extended functionalism" (e.g., Wheeler, 2010) precisely because it attempts to expand the bounds of the cognitive system beyond the biological brain. That said, it is also apparent that understanding neural implementation is crucial to generating well-founded hypotheses about brain function. Neurobiological data are particularly useful for guiding evolutionary theories by constraining our hypotheses with respect to what brains can reasonably be expected to achieve (see Colombo, 2013 and Peters, 2013). Bryant and Klasios both stick to the classical cognitivist EP party line, justifying a strategy of studying the computational-algorithmic levels alone, but we think that EP, and evolutionary approaches more generally, would benefit from using neurobiological data to inform their theoretical stance, thus grounding our knowledge in living biological systems; we are, after all, attempting to explain how such living biological systems work. Such a stance is also a natural element of the embodied perspective we endorse, which argues that the way brains are put together will matter for cognition (that is, the way that neurons, glia, neurotransmitters and neuromodulators actually go about doing their job) and how adaptive behavior in the world is generated.

From our perspective, then, it seems well-worth considering the radical non-representational/non-computational alternative proposed by Chemero (2009), as well as related work on cognitive integration. As Chemero (2009) himself points out, and as we acknowledged in our original article, embodied/dynamical approaches do not entail a rejection of all representational theories of mind. Clark (1997), for example, argues that there are certain "representation-hungry" (i.e., linguistic) processes that do not seem amenable to an account grounded in coordinated sensorimotor processes alone. Thus, there is some effort being made to reconcile embodied and dynamical approaches with computational/ representational theories (e.g., Barsalou's, 1999 "perceptual symbol systems" and Clark's, 1997 "dynamic computationalism"). At a minimum, however, the recognition of alternatives to computational-representational theories of mind make it possible to ask some penetrating questions about the nature of representation in a computational model of mind, and whether such representations are, in fact, doing all of the cognitive work, all of the time (Barrett, 2011). Thus, when Bryant (2015) asserts that cognitive integration is a computational theory he is not wrong, but nor is he right. More specifically, the issue of whether cognition is extended can be viewed as orthogonal to whether cognition should be viewed as computation (see Sutton, 2014): the issue at stake is where the bounds of the cognitive system should be drawn, and whether bodily resources, material artifacts, and other aspects of the environment can be considered constitutive parts of the cognitive system or simply causally related to them. We argued for the constitutive approach, because this follows naturally from a radical embodied view that treats cognitive processes as products of the interaction between brain, body, and environment and not the brain alone (see also Chemero, 2009; Barrett, 2011; Hutto and Myin, 2013). Even if one wishes to adhere to a computational framework, however, cognitive integration can and does represent an alternative approach to standard cognitive psychology because it views cultural artifacts (in the human case) and other environmental resources as an integral part of cognitive systems (a point made in both Barrett et al., 2014, and reiterated in Stulp et al., 2015); cognitive integration does not view the brain alone as the part that does all the heavy-lifting. To counter this, as Bryant (2015) and Klasios (2014) do, simply by insisting that brains compute is to precisely miss this point.

Loops, Not Arrows

Bryant (2015) also suggests that we have got our causal arrow largely pointing backwards. According to Bryant, culture is primarily shaped by our brains and bodies, and not vice versa (although he then goes onto suggest something very similar to our position where "the outputs of such processes feedback iteratively into an evolutionarily dynamic cultural knowledge system," which points to a tension—if not an outright contradiction—in his argument). Of course, human brains are involved in the creation and use of artifacts and other forms of cultural representation, and hence brains must be involved in the shaping of culture—this is not at odds with anything we said in our original paper. The argument from the extended mind, however, is that, by extending our cognition beyond the biological brain, we become capable of feats that would otherwise be impossible. Malafouris' (2013) recent analysis of how physical artifacts allowed us to make the transition from numerosity to a formal concept of number and hence mathematics is another good example (see also Menary, 2007). Our position, then, is that we did not get the causal arrow backwards because there is no arrow. Instead, there are loops of continual reciprocal causation, with social activities and material culture both shaping and being shaped by the brain in an ongoing cycle.

By seizing on our example of timeliness as ultimately reflecting concerns about coordination and cooperation, Bryant (2015) over-simplifies and trivializes our position. Perhaps we made our point too flippantly. What we were attempting to convey was the idea that, through our invention of hours, minutes, and seconds, along with devices to measure their passing, our specific concept of time as a fourth dimension (and so on through to the concept of space-time that characterizes Einstein's theory of relativity), has fundamentally transformed aspects of human thought and practice. There seems no way that our use of time can be reduced entirely to the demands of social coordination and cooperation. Indeed, it is interesting to note that both Basu and Waymire (2006) and Mullins et al. (2013) make exactly the reverse argument to Bryant (2015) suggesting that large-scale human cooperation was dependent on material culture, namely writing and record-keeping (although these authors argue that this allowed us to "transcend" our evolved psychology, we would suggest this represents an example of how human psychology is inherently extensive and integrated with environmental and cultural resources). Although timeliness could be a by-product of social norms and customs as Bryant suggests, the concept of time is not: our invention of various ingenious ways to measure time and how we use these to shape our lives, permit us to go far beyond anything that our Pleistocene ancestors were capable of. Of course, humans are not "infinitely flexible and unconstrained by past selection," but one has to admit there is something about the sheer inventiveness of modern human behavior that quite clearly reflects the manner in which cultural artifacts augment, enhance, and extend our evolved biological brains.

Functional Fuzziness

Bryant (2015) identifies one last failing on our part concerning the relationship between domain-generality and specificity, with reference to our argument on incest taboos. Namely, he suggests that we did not consider the possibility that unconscious mechanisms guide our behavior under such circumstances. Far from failing to acknowledge this, however, we cited Westermarck (1921) in precisely this context. It is odd that Bryant picks up on an aspect of our argument that was made explicit in our original piece, but ignores its substance, which was to counter the idea put forward by Cosmides and Tooby (1994) that incest avoidance requires innate domain-specific knowledge because such knowledge could not, even in principle, be learned. Instead, Bryant attempts to shift the emphasis, making the point that "just because a mechanism works across content domains, it is still functionally specialized. The scope of a mechanism is independent from whether it has design features." To the extent that we understand this statement, it seems to promote a rather fuzzy notion of functional specialization, and deny the very motivation for EP-style "design thinking" in the first place: that is, the notion that specialized tasks require specialized mechanisms, and cannot be solved effectively by general-purpose mechanisms that apply across several domains. Such a statement also raises an empirical worry for, if it is true that a mechanism's scope is independent of its design features, how does one go about identifying evolved functionally-specialized mechanisms applied to a new domain as opposed to evolved domain-general mechanisms operating on one of the several tasks to which they are well-suited? There seems to be no means of distinguishing the two. Consequently, when Bryant asks: where is the argument here? We would suggest that, not only is there an argument to be had, but it is one that cuts to the very heart of the EP project.

Why All the Fuss?

Summing up, Bryant (2015) suggests the gap between human behavioral ecology and EP is closing, but notes that Symons (1987) question remains: if we're all Darwinians, what's all the fuss about? For us, the fuss is about the rather restrictive view of human psychology promoted by EP, and the failure of some of its assumptions to withstand close scrutiny; a topic that occupied two-thirds of our original paper. More broadly, we think it is worth considering whether we should continue to base our model of the mind on inanimate computation (a notion that has human intentionality built into it at source) or whether we should pursue a truly evolutionary route that grounds psychology (of both human and non-humans) in living biological systems—a view that further permits the study of humans as hybrid embodied-extended biocultural beings who invent all kinds of things and so continually reinvent themselves. For us, this is another good reason why some Darwinians should continue to make a fuss.

Funding

LB is supported by NSERC Canada Research Chairs and Discovery Grant Programs; TP is supported by The Netherlands Organisation for Scientific Research (Veni scheme; 451.10.032); GS is supported by The Netherlands Organisation for Scientific Research (Rubicon Post-Doctoral Fellowship).

References

Anderson, M. L. (2015). Mining the brain for a new taxonomy of the mind. *Philos. Comp.* 10, 68–77. doi: 10.1111/phc3.12155

Anderson, M. L. (2014). *After Phrenology: Neural Reuse and the Interactive Brain*. Cambridge, MA: Bradford Books.

Barrett, L. (2011). *Beyond the Brain: How Body and Environment Shape Animal and Human Minds*. New Jersey, NJ: Princeton University Press.

Barrett, L., Pollet, T. V., and Stulp, G. (2014). From computers to cultivation: reconceptualizing evolutionary psychology. *Front. Psychol*. 5:867. doi: 10.3389/fpsyg.2014.00867

Barsalou, L. W. (1999). Perceptions of perceptual symbols. *Behav. Brain Sci.* 22, 637–660. doi: 10.1017/S0140525X99532147

Basu, S., and Waymire, G. B. (2006). Record-keeping and human evolution. *Account. Horizon* 20, 201–229. doi: 10.2308/acch.2006.20.3.201

Bryant, G. (2015). Evolved computers with culture. *Front. Psychol.* 6:498. doi: 10.3389/fpsyg.2015.00498

Chemero, A. (2009). *Radical Embodied Cognitive Science*. Cambridge, MA: MIT Press.

Clark, A. (1997). *Being There: Bring Body, Mind and World Together Again*. Cambridge, MA: MIT Press.

Colombo, M. (2013). Moving forward (and beyond) the modularity debate. A Network Perspective. *Philos. Sci.* 80, 356–377 doi: 10.1086/670331

Cosmides, L., and Tooby, J. (1994). "Origins of domain specificity: the evolution of functional organization," in: *Mapping the Mind: Domain Specificity in Cognition and Culture*, eds L. A. Hirschfeld and S. A. Gelman (Cambridge, MA: Cambridge University Press), 85–116.

Dotov, G. D., Lind, N., and Chemero, A. (2010). Demonstration of the transition from ready-to-hand to unready-to-hand. *PLoS ONE* 5:9433. doi: 10.1371/journal.pone.0009433

Gibson, J. J. (1979). *The Ecological Approach to Visual Perception*. New Jersey, NJ: Lawrence Erlbaum Associates.

Hutto, D. D., and Myin, E. (2013). *Radicalizing Enactivism: Basic Minds without Content.* Cambridge, MA: MIT Press.

Kelso, J. A. S. (1997). *Dynamic Patterns: The Self-Organization of Brain and Behavior*. Cambridge, MA: MIT Press.

Klasios, J. (2014). Our computational nature: comment on Barrett et al. *Front. Psychol.* 5:1348. doi: 10.3389/fpsyg.2014.01348

Malafouris, L. (2013). *How Things Shape the Mind*. Cambridge, MA: MIT Press.

Menary, R. (2007). Writing as thinking. *Lang. Sci.* 29, 621–632. doi: 10.1016/j.langsci.2007.01.005

Mullins, D. A., Whitehouse, H., and Atkinson, Q. D. (2013). The role of writing and record-keeping in the cultural evolution of human cooperation. *J. Econ. Behav. Organ.* 90, S141–S151. doi: 10.1016/j.jebo.2012.12.017

Peters, B. M. (2013). Evolutionary psychology: neglecting neurobiology in defining the mind. *Theory Psychol.* 23, 305–322. doi: 10.1177/0959354313480269

Rosch, E., Thompson, E., and Varela, F. J. (1992). *The Embodied Mind: Cognitive Science and Human Experience*. Cambridge, MA: MIT press.

Searle, J. (1990). Is the brain a digital computer? *Proc. Am. Philos. Assoc.* 64, 21–37. doi: 10.2307/3130074

Stulp, G., Pollet, T. V., and Barrett, L. (2015). The not-always-uniquely-predictive power of an evolutionary approach to understanding our not-so-computational nature. *Front. Psychol.* 6:419. doi: 10.3389/fpsyg.2015.00419

Sutton, J. (2014). "Remembering as public practice: wittgenstein, memory, and distributed cognitive ecologies," in *Mind, Language, and Action: Proceedings of the 36thWittgenstein Symposium*, eds D. Moyal-Sharrock, V. A.Munz, and A. Coliva (Frankfurt: Ontos-Verlag), 409–443.

Symons, D. (1987). "If we're all Darwinians, what's the fuss all about?," in *Sociobiology and Psychology*, eds C. B. Crawford, M. F. Smith, and D. L. Krebs (Erlbaum, Hillsdale, NJ), 121–146.

Thelen, E., and, L., Smith (1994). *A Dynamic Systems Approach to the Development of Cognition and Action*. Cambridge, MA: MIT Press

Wallace, B. (2007). "Introduction," in *The Mind, the Body and the World: Psychology after Cognitivism*, eds B. Wallace, A. Ross, J. Davies, and T. Anderson (Exeter: Imprint Academy), 1–32.

Westermarck, E. (1921). *The History of Human Marriage, 5th Edn*. London: Macmillan.

Wheeler, M. (2010). "In defense of extended functionalism," in *The Extended Mind*, ed R. Menary (Cambridge, MA: MIT Press), 245–270.

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

frontiers in
PSYCHOLOGY

REVIEW ARTICLE
published: 20 August 2014
doi: 10.3389/fpsyg.2014.00908

Extended evolutionary psychology: the importance of transgenerational developmental plasticity

Karola Stotz *

Department of Philosophy, Macquarie University, Sydney, NSW, Australia

Edited by:
Danielle Sulikowski, Charles Sturt University, Australia

Reviewed by:
Darren Burke, University of Newcastle, Australia
Luc-Alain Giraldeau, UQAM, Canada

Correspondence:
Karola Stotz, Department of Philosophy, Macquarie University, Sydney, 2109 NSW, Australia
e-mail: karola.stotz@mq.edu.au

What kind mechanisms one deems central for the evolutionary process deeply influences one's understanding of the nature of organisms, including cognition. Reversely, adopting a certain approach to the nature of life and cognition and the relationship between them or between the organism and its environment should affect one's view of evolutionary theory. This paper explores this reciprocal relationship in more detail. In particular it argues that the view of living and cognitive systems, especially humans, as deeply integrated beings embedded in and transformed by their genetic, epigenetic (molecular and cellular), behavioral, ecological, socio-cultural and cognitive-symbolic legacies calls for an extended evolutionary synthesis that goes beyond either a theory of genes juxtaposed against a theory of cultural evolution and or even more sophisticated theories of gene-culture coevolution and niche construction. Environments, particularly in the form of developmental environments, do not just select for variation, they also create new variation by influencing development through the reliable transmission of non-genetic but heritable information. This paper stresses particularly views of embodied, embedded, enacted and extended cognition, and their relationship to those aspects of extended inheritance that lie between genetic and cultural inheritance, the still gray area of epigenetic and behavioral inheritance systems that play a role in parental effect. These are the processes that can be regarded as transgenerational developmental plasticity and that I think can most fruitfully contribute to, and be investigated by, developmental psychology.

Keywords: extended inheritance, parental effects, developmental niche, developmental plasticity, embodied cognition, extended cognition, extended evolutionary synthesis

INTRODUCTION

There exist two quite different stances toward the evolution of human cognitive capacities. The nativist stance, favored for instance by Evolutionary Psychologists (EP), attributes the origin of behavioral, social and cognitive capacities such as folk psychology, mind-reading and general reasoning capacities to the sudden appearance of genetically determined mental modules or representational systems. This approach, which subscribes to the computational theory of mind, has been polemically dubbed the "Rational Bubble stance (which) confounds cultural symbolic achievements with individual cognitive competences" and belongs to a class of views that have in recent years come under increasing criticism as a quite unrealistic model of cognitive growth (McGonigle and Chalmers, 2008, p. 143). An alternative view, now sometimes called the *e*mbodied, *e*mbedded, *e*nactive, extended (4E) cognition approach, is united by its opposition to traditional cognitivism and methodological individualism (Menary, 2010). Despite the differences between the separate views they all seem to agree on the necessity to place active agency at the center of cognition and the importance of cognition's scaffolding through developmental, ecological, and cultural niche construction. In addition this approach presupposes only very simple and modest biological preadaptations, e.g., in the perceptual realm or general developmental plasticity (Donald, 2000a,b; Griffiths and Stotz, 2000; Tomasello, 2000; Sterelny, 2003; Wheeler and Clark, 2008; Stotz, 2010).

There is natural affinity between one's view of the nature of the mind and an understanding of how the mind developed and evolved. The Modern Synthesis—the evolutionary theory to which EP is entirely wed—almost exclusively invokes natural (including kin and sexual) selection as the driving force, genetic mutations as the creative force and genetic transmission as the only mechanism of heredity. When applied to cognition, the Modern Synthesis invites the decomposition of the mind into separately evolved cognitive traits, called mental modules, each selected to solve a particular evolutionary problem in the human ancestor's "environment of evolutionary adaptedness" (Cosmides and Tooby, 1997). The origin of these modules is explained with the appearance of certain genetic factors that code for them. Strictly speaking the modern synthesis can be understood as a theory of genes, which arguably is poorly equipped to provide a more fully-fledged explanation of the transformation of form, other than the occurrence of genetic mutations and recombinations, which somehow translate into phenotypic modifications.

There is, however, a growing consensus that we need explanatory resources that go beyond inner logical representations or the dynamics of neural networks on the on hand, and the received view of evolution on the other. Physical, social and cultural life transforms individual characteristics and abilities in daily interactions, during individual development and the evolution of the lineage. The view of organisms, especially humans as deeply integrated beings embedded in and transformed by their genetic, epigenetic, behavioral, ecological, socio-cultural and cognitive-symbolic *legacies* calls for an "extended evolutionary synthesis" (Pigliucci, 2007, 2009; Pigliucci and Müller, 2010) that goes beyond either a theory of genes juxtaposed against a theory of cultural evolution or more sophisticated theories of gene-culture coevolution and niche construction. Environments, particularly in the form of developmental environments, do not just *select for* variation, they also *create* new variation by influencing development through the reliable transmission of non-genetic but heritable information (Piaget, 1978; Gilbert and Epel, 2009; Stotz, 2010; Griffiths and Stotz, 2013). Organisms, and humans in particular, are actively engaged with and manipulate their physical and social environment and that of their descendants, which in turn not only participates in the production of selection pressures, but almost more importantly in the production of heritable phenotypic variation; therefore organisms actively contribute to their own evolution. There is a strong interconnection between be highly embodied, embedded and extended cognitive systems and the kind of developmental and evolutionary processes that bring them about (Sterelny, 2010; Stotz, 2010).

The next section will explore the alternative views of evolutionary theory that provide much richer explanatory resources for (evolutionary) psychology. It will probe which updates to the conceptual structure of evolutionary theory would be needed for its most fruitful application to problems in psychology. The next two sections will explore in more detail two issues that are of particular importance for psychology. Section Beyond Innate and Learned: the Concept of Experience criticizes the conceptual poverty created by the simplistic dichotomy between innate or genetically determined development and acquired learning. It introduces another concept, experience, as a step to bridge between and integrate development and learning. Section Extended Inheritance discusses in more detail the diverse mechanisms of non-genetic inheritance that comprise the central extension to the Modern Synthesis.

The alternative conceptions of mind and cognitions to the traditional cognitivist and computationist approach, namely 4E cognition, will stand at the center of Section Embodied, Embedded, Enacted and Extended Organisms, Extended Synthesis and Extended Evolutionary Psychology. In this final section I look in more detail at how this alternative view of the mind is related to the extended view of evolution that I have promoted here, particularly those parts of the new synthesis that I deem to have special explanatory potential for many areas of psychology. A radically different perspective to the view that sees a disembodied mind being passively molded by natural selection and genetic mutations is presented. It conceives living beings as non-linearly coupled organism-environment systems, that come with cellular, social, ecological and cultural legacies bequeathed to them from earlier generations, and who's actions substantially influence the evolutionary process.

TOWARD AN EXTENDED EVOLUTIONARY SYNTHESIS

KINDS OF EVOLUTIONARY PSYCHOLOGY

This section doesn't attempt to review, discuss and criticize in detail the main kinds of evolutionary psychology. There is an extraordinary amount of literature out there doing just that. This presents just a minimalist overview, and as such necessarily presents a bit of a caricature, the three waves of attempts to integrate psychology with evolutionary theory in the last four decades. In the seventies Edward O. Wilson attempted a "New Synthesis" under the name of Sociobiology, which viewed social behavior as the product of evolution and therefore reasoned that it should be explained in terms of adaptive success. Its arguably quite radical gene centrism, promoted particularly through Richard Dawkins' notion of the selfish gene, became the subject of intense criticism. Not entirely without intellectual connections, the nineties saw the emergence of the Santa Barbara school of Evolutionary Psychology. It applies knowledge and principles from mainstream evolutionary theory to psychology and "good old-fashioned" Artificial Intelligence/cognitive science in order to understand the design of the human mind: "In this view, the mind is a set of information-processing machines that were designed by natural selection to solve adaptive problems faced by our hunter-gatherer ancestors" (Cosmides and Tooby, 1997). This highly successful new field attracted a large number of followers over the years, but at the same time has been subjected to very vocal criticisms. Against EP's dismissal of the critics as politically motivated anti-evolutionists, many critics were biologists, philosophers of biology and psychologists motivated by a different vision of a more scientifically rigorous and a more sophisticated evolutionary psychology (see for instance Barrett et al., 2014).

The beginning of the century saw the appearance of evolutionary developmental psychology, applying evolutionary thinking to human developmental psychology: "Evolutionary developmental psychology is the study of the genetic and ecological mechanisms that govern the development of social and cognitive competencies common to all human beings and the epigenetic (gene-environment interactions) processes that adapt these competencies to local conditions" (Geary and Bjorklund, 2000, p. 57). This new field takes its inspiration from evolutionary developmental biology and so-called epigenetic theories of evolution going back to Gilbert Gottlieb in accepting a role for development, particularly developmental plasticity, in evolution (Bjorklund, 2006).

Which kind of evolutionary theory you apply matters deeply to which kind of (evolutionary) psychology you get. Therefore what follows will be a very short analysis of which kind of amendments or extensions should be included to widen the scope of problems that can be successfully addressed by evolutionary theory. Again, I have to refer to the cited literature for a much more thorough and detailed criticism and further amendment than I could present here; the present paper focuses on those new developments that in my view are most relevant for an extended evolutionary psychology.

This section asks what are the implications of recent scientific developments for the mechanisms of evolution. These developments include discoveries in molecular genetics, notably "molecular epigenesist" or "distributed specificity" of gene products, new discoveries of exogenetic heredity, and the revival of notions of epigenesis and developmental plasticity and their implications for evolution. Together with many others I have argued that these developments necessitate an extension of the conventional, neo-Darwinian theory of evolution, the so-called "Modern Synthesis." Some may argue that the referral to the Modern Synthesis presents something like a straw man argument because many practitioners have, in the intervening decades, assimilated new conceptual and methodological developments into their thinking, often perhaps without being aware to what extent some of these violate the underlying assumptions on which the original synthesis was based. Several of these assumptions are now more than three quarters of a century old, and many of the relevant theories and concepts have undergone major revisions. So the point of the call for an "extended synthesis" may be as much to think through the implications of changes that have occurred or are occurring as to call for more change (Pigliucci, 2007, 2009; Craig, 2010; Pigliucci and Müller, 2010; Stotz, 2010; Gissis and Jablonka, 2011; Griffiths and Stotz, 2013).

MOLECULAR EPIGENESIS

As stated above, the Modern Synthesis was in its core a theory of genes, but the gene that figures in it was the classical gene of Gregor Mendel and Thomas Hunt Morgan, a theoretical entity of heritable factors that permitted practitioners the "genetic analysis" of observed inheritance patterns. The knowledge of how genes conferred specificity within an organism and hence had observable phenotypic effects wasn't yet a molecular reality. Historians of molecular biology credit Francis Crick with having supplemented the existing idea of *stereochemical specificity*, embodied in the three-dimensional structure of biomolecules and underlying the well-known lock-and-key model of interaction between biomolecules, with the idea of *informational specificity*, embodied in the linear structure of nucleic acids (such as genes and other genetic elements) that determine the linear structure of a gene product (Sarkar, 1996). This idea is present in Crick's statements of his Sequence Hypothesis and the Central Dogma:

- *The Sequence Hypothesis* … In its simplest form it assumes that the specificity of a piece of nucleic acid is expressed solely by the sequence of its bases, and that this sequence is a (simple) code for the amino acid sequence of a particular protein.
- *The Central Dogma* This states that once "information" has passed into a protein it cannot get out again. In more detail, the transfer of information from nucleic acid to protein may be possible, but transfer from protein to protein, or from protein to nucleic acid is impossible. Information means here the precise determination of sequence, either of bases in the nucleic acid or of amino-acid residues in the protein. (Crick, 1958, pp. 152–153, italics in original).

Griffiths and Stotz (2013) have termed this encoding of specificity "Crick information." If a cause makes a specific difference to the order of elements in a biomolecule, it contains Crick information for that molecule. This definition embodies the essential idea of Crick's sequence hypothesis, without in principle limiting the location of biological information to nucleic acid sequences as Crick does. An important idea behind Crick information is that this causally grounded notion of biological information can be extended to apply to factors other than DNA, using research results from molecular biology. Crick's Sequence Hypothesis and Central Dogma were based on a very simple picture of how the specificity of bio-molecules is encoded in living cells. We now know that, at least in eukaryotes, coding regions are surrounded by a large number of non-coding sequences that regulate gene expression. The discrepancy between the number of coding sequences and the sometimes vastly higher number of gene products leads to the insight that the informational specificity in coding regions of DNA must be amplified by other bio-molecules in order to specify the whole range of products. Different mechanisms of gene regulation together co-specify the final product of the gene in question, first by *activating* the gene so it can get transcribed, second by *selecting* a chosen subset of the entire coding sequence (alternative splicing), and thirdly by *creating* new sequence information through the insertion, deletion or exchange of single nucleotide letters of the RNA message (RNA editing). Thus specificity, and hence Crick information, is distributed between a myriad of factors other than the original coding sequence: Non-coding DNA sequences with regulatory functions, diverse gene products such as transcription, splicing and editing factors (usually proteins), and non-coding RNAs (Stotz, 2006a,b). This leads to the second substantive use of information in contemporary molecular biology, namely in representations of genomic regulatory networks (GRNs) as implementing computations (Kauffman, 1969; Davidson and Levine, 2005).

Specificity turns out to be not inherent in any single biomolecule in these large networks but induced by regulated recruitment and combinatorial control (Ptashne and Gann, 2002). And it is here that we will find that the networks cannot be reduced to DNA sequences and gene products, because many of the latter need to be recruited, activated or transported to render them functional. These processes, the recruitment, activation, location or transportation of transcription, splicing and editing factors, allow the environment to have very *specific* effects on gene expression. I believe that this is a way to give a more precise meaning to the distinction between "instructive vs. permissive environmental causes" (Gilbert, 2003; Gilbert and Epel, 2009). Many regulatory gene products serve to relay environmental (Crick) information to the genome. While in embryology and morphogenesis it is often acknowledged that environmental signals play a role in the organization of global activities; they are rarely seen to carry information for the precise determination of the nucleic acid or amino acid chains in gene products. But this is precisely what occurs. Not just morphogenesis at higher levels of organization, but even the determination of the primary sequence of gene products is a creative process of "molecular epigenesist" that cannot be reduced to the information encoded in the genome alone (Stotz, 2006b; Griffiths and Stotz, 2013).

Section Beyond Innate and Learned: the Concept of Experience will argue that these developments warrant the introduction of another concept in psychology, namely "experience," beside the concepts of development and learning, to accommodate the many different avenues by which an organism reacts to and interacts with the environment.

NON-GENETIC INHERITANCE

Evolution is defined as changes in gene *frequencies*, because only the base sequence was deemed hereditary. The idea that developmental outcomes could be transmitted to the next generation was for almost a century discredited as raising the specter of Lamarckism. The molecular discoveries of epigenetic mechanisms, which produce effects on gene expression that were not just heritable from one cell to the other but in certain cases also from parent germline to offspring germline, however, have rendered ideas of non-genetic or exogenetic inheritance respectable. Parents beget their children not just gene *sequences* but also instructions over gene *expression* and other functional states. In addition, many aspects of the environment and individual experiences of a developing organism are there by evolutionary design: "genes *inherit* a rich and supportive environment, a fact few dispute but few discuss with any urgency" (West and King, 1987, p. 552, italics added). Evolution has designed not only a reactive genome, but also a "developmental niche" co-constructed by the parental and offspring generations to which the genome reacts to reconstruct life-cycles (see Section Developmental Niche Construction).

Since the development of molecular epigenetics has brought the existence of exogenetic inheritance to the attention of a much larger field, the idea is slowly gaining wider acceptance. The main points of debate today concern the scope and potential mechanisms of transgenerational transfer of non-genetic information, and its importance for evolutionary dynamics. Epigenetic inheritance proper, transmitted through the germline, and behaviorally transmitted transgenerational epigenetic effects (see Section Extended Inheritance) differ in several important ways from genetic inheritance: epigenetic variations may be less stable, because these variations are in principle reversible, and many organisms have developed safeguards against their transgenerational transmission. These features are not necessarily a disadvantage: in comparison to genetic inheritance, epigenetic mechanisms are more sensitive to the environment, which might make them more directed, more predictable, and also more flexible. These are all features which potentially render them more adaptive in the short term than blind genetic variation, particularly in variable environmental conditions (Jablonka and Lamb, 1995; Holliday, 2006). Exogenetic inheritance systems often transfer information involved in 'adaptive transgenerational plasticity' (see Section Transgenerational Developmental Plasticity: Parental Effects):

> . . . because the parental phenotype responds to some aspect of its environment that correlates with a feature that is of adaptive relevance to the offspring. This correlational information can be exploited by developmental processes because of the continuity between parental and offspring phenotypes (. . .). In genetic inheritance systems, on the other hand, correlational information requires a process of selection that builds up gene frequency differences between environments. (Uller, 2012).

DEVELOPMENTAL PLASTICITY AND EVOLUTION

There are now a variety of scientific fields interested in the extent to which development influences evolution, and the ideas about which mechanisms are evolutionarily relevant differ greatly: The most radical position asserts that environmentally induced and developmentally regulated variation in exogenetic, developmental resources may be transmitted directly to the next generation either from germ or soma cell to germ cell, or from soma to soma, in order to create heritable variation in the phenotype (Griffiths and Gray, 1994; Jablonka and Lamb, 1995, 2005; Stotz, 2008, 2010; Stotz and Allen, 2008; Badyaev and Uller, 2009; Gilbert and Epel, 2009; Danchin et al., 2011; Bonduriansky, 2012; Uller, 2012).

Some biologists insist that only epigenetic inheritance transmitted through the gametes should be called a proper inheritance system, while the transmission from soma to germline or soma to soma is described as "transgenerational epigenetic effects" (Youngson and Whitelaw, 2008). Bonduriansky (2012) has argued that this resistance stems from the forceful association between genes and biological inheritance created by transmission genetics. For others less impressed by those historical developments transgenerational epigenetic effects are parental effects mediated via epigenetic mechanisms, which fall under the behavioral inheritance system (e.g., Meaney, 2001; Danchin et al., 2011; Griffiths and Stotz, 2013). Some evolutionary developmental biologists, traditionally reluctant to accept the existence of non-genetic inheritance, now embrace the importance of epigenetics for evolution, but see it as an extension of the genetic inheritance system since it works via the modification of the chromatin system, which forms part of the chromosome (Hallgrimsson and Hall, 2011).

According to others, phenotypically plastic responses during the lifetime (phenotypic accommodation) may uncover the existence, or facilitate the production, of suitable genetic change. Such genetic variation may lead via natural selection to either genetic assimilation (also known as the Baldwin effect), or genetic accommodation, in other words the genetic inheritance of either decreased or increased responsiveness to environmental conditions (Waddington, 1953a,b; West-Eberhard, 2003). Others argue that a group of conserved core processes of organisms facilitate the generation of phenotypic variation out of underlying genetic variation, called "facilitated variation" (Kirschner and Gerhart, 2010). Approaches closely related to the idea of facilitated variation maintain that evolution should be understood as a succession of developmental life cycles rather than change in gene frequencies, and it is therefore developmental mechanisms that provide the necessary causal explanations for how genetic change translates into phenotypic modifications (Hall, 1999).

Lastly, there are those within the niche construction (Odling-Smee et al., 2003) and the gene-culture coevolution approaches (Boyd and Richerson, 1985) who maintain that individual behavior and hence development influences evolution mainly by affecting the future selection pressure of the population through ecological and cultural niche construction activities. These modified selection pressures then feed back to evolutionary processes.

SUMMARY

The most important difference between the received view and an extended synthesis as conceived here is the acceptance of inheritance as a much wider phenomenon than originally understood. Inheritance is hence defined as the parental transfer to the next generation of all the developmental resources, including but not limited to DNA, that permit the reconstruction and modification of the developmental system. This developmental system is the whole organism-developmental niche complex. This reconstruction and modification encompasses both developmentally entrenched effects as well as sources for the expression of novel phenotypic variation, a case of potentially adaptive transgenerational plasticity. Some parental effects (see below) enable the persistence and even the spread of the induced phenotype by modifying selection pressure (e.g., when parental resources such as protection contribute to the offspring's ability to survive and reproduce).

So, while many still argue to what extent the transference of non-genetic resources influences population dynamics and the rate and direction of phenotypic evolution, here I want to advocate to want to advocate the extent to which it can provide more adequate answers to a wide range of central evolutionary questions (questions modified from Pigliucci and Kaplan, 2006). These include the:

a. Origin of novel traits: adaptive transgenerational plasticity.
b. Modification of traits: environmentally induced variability via parental effects.
c. Spread of traits: the co-construction of a selective environment by developmental systems (selective niche construction).
d. Maintenance of traits: stabilization of the developmental and selective niche.
e. Reliable (re)production of traits: entrenched extended inheritance mechanisms (developmental niche construction) (compare Stotz, 2010).

BEYOND INNATE AND LEARNED: THE CONCEPT OF EXPERIENCE

Section Extended Inheritance will look in more detail at a range of mechanisms of, and fields of research into, non-genetic inheritance, in particular epigenetic inheritance both in its narrow and wider meaning, parental effects on offspring phenotype, and the idea of the developmental niche, which is constructed by these processes.

But before that, the root of some conceptual shortcomings in psychology—and beyond—needs to be addressed. This is the conceptual poverty expressed in the commonsense distinction between the innate and the acquired, usually decoded as caused by genes vs. being the product of learning (see Stotz and Allen, 2012 for a more detailed analysis of this problem). Unlike in biology, in wide areas of psychology the process of learning, instead of being understood as part and parcel of behavioral development, is set against the maturational, preprogrammed unfolding of the young to the adult.

A clarification of the relationship between the concepts of learning and development in psychology will require a *biologically informed* psychology, and the formulation of a broadened concept of "experience" may help to bridge the gap between learning and development by including all aspects of environmental stimuli that lead to long-term adaptive changes of behavior, including "learning" in its usual narrower sense. In other words, the concept of experience is not limited to sensory processing but includes a quite heterogeneous mix of environmental resources influencing the system's behavior. While this concept is not new, it unfortunately is not commonly used in scientific investigations, other than in its fields of origin (early comparative psychology and developmental psychobiology). My understanding of experience follows its original definition by the American animal psychologist Theodore Christian Schneirla, quoted by his student Daniel Lehrman: "Experience is 'the contribution to development of the effects of stimulation from all available sources (external and internal), including their functional trace effects surviving from earlier development' (Schneirla, 1957). Within this wide range of processes learning is only a relatively small part" (Lehrman, 1970, p. 30). To take this really on board one needs to acknowledge that physiological regulation and the regulation of behavior cannot be sharply separated, since their underlying mechanisms do not necessarily belong to distinctly different classes. This is especially so in early development. Reintroducing the concept of experience is not another way of saying that all behavior is learned, but a vehicle to bring home the inadequacy of the distinction between innate and acquired. It implicitly questions why "instinct" and "learning" should be the only two choices available to us for understanding behavioral development. A necessary requisite for the integration of the concepts of learning and development is to understand development as proposed by the developmental systems theory (Oyama et al., 2001).

The last decade has witnessed enormous scientific advances in genomics, systems biology, social neuroscience, evolutionary, and ecological and developmental biology ("evo-devo," "eco-devo," phenotypic plasticity, niche construction, extra-genetic inheritance, developmental systems theory). They challenge overly gene-centered and pre-deterministic as well as environmentalist explanations of behavior. Nature and nurture don't interact as if they were separated entities, with nature as the *a priori* plan being separated from concrete living and nurture being the means for modifying nature's plan through experience. Instead, every trait develops out of the nonlinear interaction between a range of very diverse developmental resources that cannot be usefully divided into genetic and non-genetic resources. It starts with the environmental regulation of gene expression, goes over a range of experiences beneath the skin and above the gene, over stages of sensory and social learning in vertebrates, to the exquisitely sensitive learning capacities of the human brain. "Nurture" is this ongoing process of development, while "nature" is the natural outcome of the organism-environment-system (Oyama, 1999).

Do we find learning or cognition in bacteria? The answer depends very much on your definition of learning and experience. Possibly yes, if "environment" is understood as the source of a "quite heterogeneous mix of resources called experience" (Moore, 2003, p. 350) extracted by a wide variety of means, only one of which is sensory, and if means for behavior derive from more than what is known to the senses. The concept of bacterial learning is no mere philosophical abstraction because of the many shared molecular pathways, often down to prokaryotes. For example, the NMDA receptors involved in the synaptic plasticity of neurons use proteins for binding amino acids that are highly conserved from bacteria (Kuryatov et al., 1994).

The study of behavior and cognition looks at three interconnected time-scales: evolution, development, and situated behavior. The integration of the first two seems possible now, and there are successful attempts at integrating the second two in areas of psychology, namely developmental psychobiology and social neuroscience (Michel and Moore, 1995; Cacioppo et al., 2002). This integration is based on an essential role for biology in psychology. From a psychobiological perspective, learning appears as a category within an overall framework of development as the lifelong, adaptive construction of the phenotype in its environment. Taking the idea of phenotypic plasticity seriously could, on the other hand, lead to a conception of development as a lifelong process of "learning" or "acquiring" an adaptive mode of living in a partially constructed environment.

EXTENDED INHERITANCE

MECHANISMS OF TRANSMISSIONS: FOUR INHERITANCE SYSTEMS

Eva Jablonka and Marion Lamb propelled the idea of epigenetic inheritance to prominence with their provocative title *Epigenetic Inheritance and Evolution: The Lamarckian Dimension* (Jablonka and Lamb, 1995). Epigenetic inheritance in this context is used primarily in its narrow sense as the inheritance of cellular functional states via structural elements (e.g., membranes), steady-state systems (self-perpetuating metabolic patterns), and chromatin modification (chemical modifications of histone proteins or DNA bases), although it often spills over into a broader sense to include other exogenetic inheritance systems. Jablonka and Lamb's identification of epigenetic inheritance with the inheritance of acquired characters is not unproblematic. Some scientists insist that the term Lamarckian inheritance should be restricted to the inheritance of phenotypic (somatic) characters that are acquired during development (Hall, 2011, p. 11). It would also entail a directed response to the environment, not just blindly caused by it. While strict epigenetic inheritance is transmitted through the germline, it is often mixed up with "experience-dependent epigenetic inheritance" (Danchin et al., 2011) in the broader sense, which should really be understood as behavioral and ecological inheritance mediated by epigenetic effects. As said above, the latter form has also been termed transgenerational epigenetic effects (Youngson and Whitelaw, 2008). The problem may often be that the exact underlying mechanism for a parental effect is not yet known. Epigenetic inheritance of the latter kind may also have distinctive evolutionary advantages. Particularly the parental effect literature offers a wide range of examples where parental effects, that work later in development and are mediated by the latter kind of epigenetic effects, enable the development of functional phenotypes in the offspring (Uller, 2012).

Some molecular biologists have argued that one should speak of epigenetic inheritance in the literal sense only in those cases when the methylation pattern is transmitted unchanged over several generations (Wilkins, 2011, p. 391). Some cases certainly meet this criterion. In a comprehensive review of epigenetic inheritance Jablonka and Raz conclude that it is ubiquitous, and can show stability of transmission of up to 3 generations in humans and up to 8 generations in other animal taxa, while plants can have a very stable epigenetic transmission (Jablonka and Raz, 2009). Many cases, however, would indeed not meet the criterion of multi-generational transmission. Epigenetic signals are very sensitive to environmental factors in that they are first "established by transiently expressed or transiently activated factors that respond to environmental stimuli, developmental cues, or internal events" (Bonasio et al., 2010, p. 613). That doesn't mean that we should accept the criterion of multi-generational stability. Several hypotheses about the evolutionary origins of epigenetic inheritance stress its value in spatially and temporally heterogenous environments, where it allows rapid responses to change. It is simply not correct that epigenetic change will only affect evolution if the changes themselves persist for more than one generation. Parental effects researchers have long known that one-generation parental effects substantially alter the dynamics of evolutionary models by changing which equilibrium a population will evolve to (Wade, 1998). In conventional quantitative genetics, the importance of Mendelism is not that individual genes can be tracked from one generation to the next—quantitative genetics does not do this—but that Mendelian assumptions let us work out what phenotypes (and hence their fitness) will appear in the next generation as a function of the phenotypes in the last generation. Epigenetic inheritance changes that mapping from parent to offspring, and this will affect evolution. There is no more central instance of the study of heredity than quantitative genetics, so more argument is needed for why epigenetic inheritance needs to be stable for several generations to be regarded as a form of heredity.

As I mentioned above, discussion of epigenetic inheritance often spills over from discussion of the specific phenomena of meiotic inheritance of chromatin modifications to include other phenomena that produce a parental effect. This is understandable, because molecular epigenetic mechanisms are often important in parental effects that do not involve actual epigenetic inheritance. For example, in one well-studied example, epigenetic mechanisms have been shown to mediate the transgenerational effect of maternal care in rats without actual epigenetic inheritance. Maternal behavior establishes stable patterns of methylation in the pups. These affect brain development and the behavior of the next generation of mother rats. While the behavior of those mothers reestablishes the patterns of methylation, they are not inherited through the germline (Meaney, 2001; Champagne and Curley, 2009). So long as the environment is constant, or the epigenetic pattern is maintained throughout the lifetime of the parent and reliably programs parental behavior, the phenotype will remain constant through many generations. The authors call this environmental programming of certain types of behavior through DNA methylation "life at the interface between a dynamic environment and a fixed genome" (Meaney and Szyf, 2005).

In a recent book, Jablonka and Lamb have attempted to organize the topic of epigenetic inheritance in this wider sense around four "dimensions" of heredity: Genetic, Epigenetic, Ecological, Behavioral and Cultural, and Symbolic (Jablonka and Lamb, 2005). The Genetic Inheritance System comprises protein coding and non-coding RNA genes plus the regulatory motifs in the genome, as well as sequences with unknown functions. The Epigenetic Inheritance System includes modifications of DNA and chromatin, which are part of the nucleus. Beside these resources that are literally physically attached to the genome other developmental resources are transmitted through the cytoplasm of the egg, such as parental gene products (regulatory proteins and non-coding RNAs). The cortical inheritance system consists of cellular structures such as organelles with their own membranes and genes (mitochondria and chloroplasts), membrane-free organelles (ribosomes and the Golgi apparatus), and the cellular membrane systems. Most of these structures cannot be produced from genetic information alone but act as templates for themselves. A Behavioral (plus cultural and ecological) Inheritance System forms a third dimension, in which information is transmitted through behavior-influencing substances, non-imitative and imitative social learning, as well as habitat construction, food provisioning, and other parental effects like that described in the last paragraph. The Symbolic (plus the Cognitive) Inheritance System forms the last dimension. Offspring inherit social structures and rules, cultural traditions and institutions, and technologies. This inheritance system importantly includes epistemic tools, such as language, competent adults, teaching techniques etc. (compare Jablonka and Lamb, 2005). All systems use different mechanisms of transmission and show changing degrees of fidelity. Some mechanisms may not be intrinsically stable. The nuclear genetic inheritance system, for example, relies on several layers of proof reading and copy-error detection systems for its exceptionally high fidelity. A suitable mechanism of scaffolding can lend the transmission mechanism reliability: proof reading supports genetic inheritance, epigenetics stabilizes gene expression. Learning is scaffolded by teaching or by the reliable affordances of stimuli "that define what is available to be learned . . . (and) . . . function to channel malleability into stable trajectories" (West et al., 2003, p. 618).

As already mentioned, apart from its quite clearly defined molecular sense, epigenetic inheritance can also mean something much more general and much less clearly delineated. This other meaning derives in part from Waddington's original understanding of epigenetics, but also tries to integrate newer developments and understanding:

> Epigenetics . . . focuses on the general organizational principles of developmental systems, on the phenotypic accommodation processes underlying plasticity and canalization, on differentiation and cellular heredity, on learning and memory mechanisms. Epigenetics includes the study of the transmission to subsequent generations of developmentally-derived differences between individuals, thereby acknowledging the developmental aspect of heredity. (Jablonka, pers. comm., cited in Gottlieb, 2001).

TRANSGENERATIONAL DEVELOPMENTAL PLASTICITY: PARENTAL EFFECTS

Amongst the oldest of the research agendas investigating processes of transgenerational transmission of nongenetic resources is work on "parental effects." As its name suggests work of this sort does not start from findings about underlying mechanisms. Instead, it begins with the relationship between parent and offspring phenotypes. Parental effects are sustained influences on offspring phenotype that are derived from the parental phenotype beyond the nuclear genes bequeathed to the offspring. The parental phenotype is the result of genetic, environmental and (grand-) parental effects, and their interaction. More formally, we can say that a parental effect is a correlation between offspring and parent phenotypes that is statistically independent of the correlation between their genotypes.

Parental effects are received as part of the environmental component of offspring phenotypes. The environment provided by the mother for her offspring is a very important factor in causing fitness differences among newborns and weanlings, particularly in organisms with extensive parental care. In environmentally induced parental effects the environment experienced by the parental generation influences the phenotype of the offspring. In locusts, an environment overcrowded with conspecifics experienced by the mother causes her to coat her eggs with a hormonal substance containing serotonin, which induces the egg to develop into a high-density morph with wings and legs suitable for migration. Many parental effects, like this one, enhance the offspring's fitness. Natural selection has shaped offspring to respond to subtle variations in parental behaviors or parental provisioning as a forecast of the environmental conditions they will ultimately face after independence from the parent (Mousseau and Fox, 1998; Maestripieri and Mateo, 2009). The organism's developmental plasticity utilizes environmental cues or developmental resources inherited from the parents to fine-tune its phenotype to the current or expected environment.

Because parental effects are defined phenomenologically—an observable relationship between phenotypes, any mechanism that produces this relationship counts as a parental effect. The domain of phenomena called parental effects includes narrow-sense epigenetic effects that are reproduced in meiosis and thus can pass from one generation to another, but it includes many other things as well. The mechanisms that can create a parental effect include: parental gene products (mRNAs, ncRNAs, proteins); cytoplasmic inheritance (mitochondria, plastids, membranes, signaling factors, chemical gradients, intra-cellular symbionts; often investigated separately as maternal inheritance); oviposition (the placement of eggs in insects, fish, and reptiles can effect food availability and quality, temperature and light conditions, and protection against predators and other adverse conditions, and hence has important consequences for the fitness of the offspring); gut organisms (which are often necessary for the normal development of intestines and the immune system, and daily metabolism); sex determination (via maternal influence on temperature exposure in reptiles, hormonal influence on gamete selection in birds); nutritional provisioning (prenatally through seeds, eggs, and placenta, postnatal feeding particularly in mammals and birds, that not only provides sustenance for the offspring but influences later food preferences, feeding behavior, and metabolism); parental care and rearing practices (warmth, protection, and emotional attachment, e.g., differential licking in rats, teaching and learning); social status (in hierarchically organized mammals, such as primates, offspring often inherit the social status of the mother), among other things (Mousseau and Fox, 1998; Maestripieri and Mateo, 2009). Although most of these phenomena do not count as narrow-sense epigenetic inheritance, because they do not involve the transfer of chromatin modifications through meiosis, the phrase "epigenetic inheritance" is sometimes used in a wide sense that is more or less equivalent to parental effects. The reason is that they often assert their effect on the phenotype via epigenetic mechanisms caused by the maternal phenotype. I prefer to use the less ambiguous phrase exogenetic inheritance in those contexts where the exact underlying mechanisms are not yet known.

As might be expected from such a diverse field, there are many different approaches to parental effects. Parental effects researchers Badyaev and Uller (2009) have shown how the differences in the ways parental effects are understood reflect the different roles they play in research. These different approaches do not necessarily count exactly the same phenomena as parental effects. For many geneticists it is essentially a statistical concept, i.e., an additional parent-offspring correlation that must be added to a quantitative genetic model in order to correctly predict the effects of selection. In contrast, someone studying animal development is likely to define parental effects at a mechanistic level, referring to specific ways in which they are produced. Evolutionary biologists see parental effects either as adaptations for phenotypic plasticity, or as the consequence of a conflict between parent and offspring seeking to influence each other's phenotype to suit their own interests:

> . . . parental effects mean different things to different biologists—from developmental induction of novel phenotypic variation to an evolved adaptation, and from epigenetic transference of essential developmental resources to a stage of inheritance and ecological succession. (Badyaev and Uller, 2009, p. 1169).

I suggest that the distinctive feature of parental effects is that it is a phenomenological concept. So parental effects should not be defined by any specific mechanism that brings them about. Second, parental effects should not be defined as adaptations, since their evolutionary significance does not depend on this—the correlations have the same impact on the dynamics of evolution whether or not they are adaptations. From a developmental perspective, parental effects need to be understood before the difficult question of their evolutionary origins can be properly addressed. More importantly, non-genetically inherited resources shouldn't be understood as competing with genetic resources; they complement them. They do this in part by amplifying the sequence information encoded by nucleic acids, as summarized by the idea of molecular epigenesis. Badyaev and Uller summarize the significance of parental effects in development and evolution very nicely:

> Here, we suggest that by emphasizing the complexity of causes and influences in developmental systems and by making explicit the links between development, natural selection and inheritance, the study of parental effects enables deeper understanding of developmental dynamics of life cycles and provides a unique opportunity to explicitly integrate development and evolution. . . .parental effects on development enable evolution by natural selection by reliably transferring developmental resources needed to reconstruct, maintain and modify genetically inherited components of the phenotype. The view of parental effects as an essential and dynamic part of an evolutionary continuum unifies mechanisms behind the origination, modification and historical persistence of organismal form and function, and thus brings us closer to a more realistic understanding of life's complexity and diversity (Badyaev and Uller, 2009, p. 1169).

DEVELOPMENTAL NICHE CONSTRUCTION

The concept of the ontogenetic niche was introduced in 1987 by developmental psychobiologists Meredith West and Andrew King. It provides a way to bring together the research agendas described above that focus on exogenetic inheritance mechanisms in the widest sense. Many aspects of the environment and experience of a developing organism are there by design: Evolution has designed not only a reactive genome, but also a developmental niche that reacts with it to construct phenotypes. West and King define the ontogenetic niche as a set of ecological and social circumstances inherited by organisms (West and King, 1987, p. 550). One should add epigenetic, epistemic, cultural, and symbolic legacies to this list and point to Jablonka and Lamb's "dimensions" of heredity as a thorough and principled effort to taxonomize the contents of the developmental niche (Jablonka and Lamb, 2005; Stotz, 2006c, 2008, 2010; Griffiths and Stotz, 2013). Naturally, some dimensions are more prominent in one taxon than another. Together, these legacies are designed to provide the developmental resources needed to reconstruct and modify the life-cycle in each generation. The developing organism can expect to encounter this niche in development as reliably as it does its genome: "It's the dependability of the niche in delivering certain resources to the young that makes it a legacy" (West et al., 1988, p. 46).

The developmental niche provides an alternative to the nature-nurture dichotomy (Stotz, 2008; West and King, 2008). The niche equals nurture since it nurtures the developing organism, and it equals nature (traditionally understood as the innate), because it is part of the organism's endowment. West and King and their collaborators devoted decades of painstaking research to the acquisition of species-typical behavior of the Brown-headed Cowbird. As a nest parasite the cowbird had been assumed, since it could not learn species-specific behaviors from its parents, to inherit those behaviors genetically: they are innate. West and King set out to show that this kind of dichotomous thinking was no substitute for a causal analysis of how the phenotypes actually develop. The results of this research led them to develop the "ontogenetic niche" concept. The ability of cowbirds to recognize their own species visually depends, amongst other factors, on "phenotype matching"—individuals seek to interact with birds that look like themselves. This, in combination to ecological factors, helps ensure that cowbirds find themselves in flocks. Male song is shaped by feedback from female cowbirds, whose wing stroking and gaping displays in response to the songs strongly reinforces males (West and King, 2008). Raised in isolation males will sing, but they need feedback from a mature female audience and also competition with other males in order to learn how to produce cowbird songs in a way that lead to successful mating:

> In cowbirds the juvenile niche is a forum in which males learn the pragmatics of singing, which appears to be a performatory, if not sometimes martial, art. (West and King, 1987, p. 52).

Female song preferences are themselves socially transmitted. As a result, cowbirds reliably transmit not only species-typical songs, but also regional song dialects. The flock functions as an information center, controlling what is "bioavailable" to be learned throughout the lifespan. The developmental niche concept undermines the traditional dichotomy between heredity and individual experience, since it highlights how experience, including in some taxa real social learning, is involved in the development of species-typical behavior. Aspects of experience are part of the mechanism of heredity (West and King, 2008).

The cowbird is not an isolated example. Other examples in which developmental niches afford the robust experiences necessary for normal development include food and habitat imprinting in insects through oviposition; maternal care and stimulation for neural development (sexual behavior and fear reaction in rats; learning disposition in chickens); territorial and habitat inheritance (nest sites, food resources, a hierarchy of relatives) in woodpeckers and jays; maternal rank inheritance in carnivores and primates (Maestripieri and Mateo, 2009).

Jeff Alberts has used the developmental niche extensively in studies of rat development. The rat pup passes through four consecutive "nurturant niches" on the way to adulthood: the uterine niche, the dam's body, the huddle in the natal nest, and the coterie (Alberts and Schank, 2006). They all provide sustenance for the developing organism, such as nutrients, warmth, insulation, and "nurture" in the form of behavioral and social stimuli as affordances for development. The early ontogeny of species-typical rat behavior is directed mainly by olfactory, but also tactile, cues that are provided by the different ontogenetic niches. Olfactory cues on the dam's nipples guide the pup to them. However, the pup's developing sensoria need to acquire odor recognition of the nipple through chemical cues in the amniotic fluid provided by the uterine niche it had passed through before. The spread of amniotic fluid over the dam's body after birth bridges the pre- and postnatal niches of the pup. Filial huddling preferences in the natal niche are mediated by learned olfactory cues provided from the close proximity of the siblings during the suckling stage. This huddle or natal niche in turn induces preferences prerequisite for the functioning of the rat in the social context of the "coterie niche," through thermotactile stimulation. Alberts notes:

> Again we find a stereotyped, species-typical, developmentally-fixed behavior is learned, with all of the key components [...] existing as natural features of the ontogenetic niche. ... Specific features of these niches elicit specific reactions and responses in the developing offspring. (Alberts, 2008, p. 300).

These niches afford the pups a range of other experiences. In the previous section we encountered Michael Meaney and collaborators' discovery that natural variation in maternal care, elicited by experiences of the mother, influence stress responses, exploratory and maternal care behavior in the offspring. The quality of the mother's licking and grooming behavior results in a cascade of neuro-endocrine and epigenetic mechanisms. One pertinent example is the permanent down-regulation in the expression of the glucocorticoid receptor gene in the pup brain's hippocampus via the methylation of its promoters, which occurs in response to a low-level of licking and grooming by the mother (Meaney, 2001; Champagne and Curley, 2009). This down-regulation causes high stress-reactivity in the offspring. Hence stressful mothers in reaction to an adverse environment produce stressful daughters who in turn become stressful mothers. This is not necessarily bad, since highly stressed individuals are better prepared to survive in adverse environments (e.g., a high level of predation). Conversely, relaxed mothers that show a high level of licking and grooming produce relaxed offspring that turn into high licking mothers. Experiences can help to construct the legacy that the next generation will receive: "Exogenetic legacies are inherited, but they are also learned" (West et al., 1988, p. 50).

The developmental niche explains the reliable development of species-typical features, but the framework is equally applicable to plastic phenotypes. Many developmental systems are "designed to be as open as ecologically possible and thus immediately sensitive to ecological change" (West and King, 2008, p. 393). The niche contains the scaffolding for normal development, but the genome has coevolved with the niche and can also use it as a source of information for developmentally plastic responses: "Animals have evolved to integrate signals from the environment into their normal developmental trajectory" (Gilbert and Epel, 2009, p. 9). The fact that development is not laid out before it occurs, with other causal factors as merely permissive (or disruptive), but instead emerges through a process of epigenesis, is what enables the integration of robustness and plasticity in development (Lamm and Jablonka, 2008; Bateson and Gluckman, 2011).

EMBODIED, EMBEDDED, ENACTED AND EXTENDED ORGANISMS, EXTENDED SYNTHESIS AND EXTENDED EVOLUTIONARY PSYCHOLOGY

In the introduction I alluded to the interplay between the nature of the organism and mechanisms of evolution. This section will explore this relationship in more detail. While what kind of mechanisms one deems central for the evolutionary process deeply influences one's understanding of the nature of organisms, adopting a certain approach to the nature of life and cognition and the relationship either between the two or between organism and environment should affect one's view of evolutionary theory.

One perspective views species of organisms as passively molded by external selection working on the random mutations organisms possess, with the evolutionary process pretty much unaffected by the behavior of organisms themselves (or so the equations at the heart of evolutionary theory, population genetics, imply). A radically different perspective views living beings as non-linearly coupled organism-environment systems, whose actions substantially influence the evolutionary process via two different pathways: the developmental creation of potentially directed or adaptive variations, and the active construction of the population's niche and hence the selection pressures acting on it. Under the latter perspective it shouldn't matter if you start with a revised vision of the nature of life and cognition or a revised vision of the nature of the mechanisms that underlie the process of evolution. One should prescribe the other.

DISEMBODIED MINDS AND THE MODERN SYNTHESIS

The modern synthesis asserts that mutation in genes provide the only (and, at that, blind and non-directed) variations and the slow process of natural selection acting on these variations is its direction-giving, order-producing or creative force. Genetic variations determine the organism's characteristics, which in turn influence its fitness, i.e., its ability to survive and reproduce. Genetic inheritance renders these fitness differences hereditary. Since evolution is defined as changes in gene frequencies, it is implied that development, including potential developmental modifications through phenotypic plasticity or the behavior of organisms, plays no role in this process. The causes of phenotypic variation, evolution's main currency, are solely genetic: blind mutation, sexual recombination, genetic drift and gene flow. Additionally, natural selection is the result of hostile external forces on populations, a "struggle for existence" which results in the "survival of the fittest." Both take place without any acknowledged influence of the organism—with the notable exception of sexual selection, already envisioned by Darwin as a secondary mechanism of selection, which is greatly influenced by the choice of an organism's choice of sexual partners. In the seventies, ideas of evolutionary game theory, the competition between different genetically inherited strategies of survival and reproduction, were added. Today we also have theories of coevolution, such as gene-culture coevolution, and niche construction. These theories all work by recognizing that populations influence, to some extent, their own selection pressures. The main reason for this relative neglect of the organism in the modern synthesis was that any influence by the developing organism that is not originally caused by its genetic make-up was assumed to not leave any trace effects on its descendants. And so it comes as no surprise that the main equations in population genetics, the formal backbone of the modern synthesis, calculate frequency and interaction of alleles and genes in populations, without any mention of the organism.

THE ROLE OF EMBODIED, EMBEDDED AND EXTENDED ORGANISMS IN AN EXTENDED EVOLUTIONARY PSYCHOLOGY

The adapted mind of evolutionary psychology has a cognitive foundation of innate, content-rich mental modules, supposed to be universally shared by all humans. EP proposes that strong selective pressures during the ancestral environment of evolutionary adaptedness (EEA) have accounted for the evolution of these faculties, shaped by environmental problems of the human's ancestor in the Pleistocene. They include not only sets of rules and algorithms for problem-solving and other mental faculties, but consist of concrete information reflecting the structure of the real world at the time when our mental capacities were meant to have evolved.

The alternative view of evolution as the "change in the distributions and constitution of developmental systems" does not posit a population of static and passive entities. Instead of random mutations and drift, developmental plasticity produces variable and active organisms that engage with their environment. The core of heredity, one of the main supporting beams of the received view, doesn't have to be the persistence of traits due to un-interrupted channels of genetic transmission. Instead, self-organizational properties of the system actively create and construct both stability (heredity) and variability (adaptability) through the availability of developmental resources in every generation. **Table 1** describes the main tenets of an Extended Evolutionary Synthesis as sketched earlier in the paper.

As argued here, an extended evolutionary theory is reciprocally related to the view of a cognitive system as embodied, embedded, enacted, and extended, promoted recently by many proponents in cognitive science. There are plenty of older thinkers who have promoted similar ideas and present therefore part of the heritage of this view[1]. For the particular argument in this section, and indeed this paper, which are related to the relationship between biological development and evolution with a view of cognition, a very important proponent has been Jean Piaget. His main subject of study was the origin of knowledge:

> Of course the most fruitful, most obvious field of study would be reconstituting human history—the history of human thinking in prehistoric man. . . . Since this field of biogenesis is not available to us, we shall do as biologists do and turn to ontogenesis. (Piaget, 1970, p. 13).

Table 1 | A comparison between the modern and the extended synthesis.

Evolutionary mechanism	Modern synthesis	Extended synthesis
Variation	Mutation, recombination	Mutation, recombination, developmental plasticity, variability
Inheritance	Genetic inheritance	Genetic (incl. assimilation and accommodation), epigenetic, ecological, behavioral/cultural, symbolic inheritance; parental effects, developmental niche construction
Natural Selection/adaptation	Independent external force on population	Niche construction Complex adaptive systems; adaptability; evolvability
Adaptation	Genetic solution to environmental problem	Active mind in active body embedded in world
Development	Genetic program	Interactive construction, developmental niche
Organism	Passive object in hostile world	Active agent in own evolution

---

[1] There are indeed many differences between the different views, such as between enacted and extended, or embodied and *radical* embodied cognition. For the argument of this paper, however, the many facets of these views and where and how they disagree with each other should not concern us.

In painstaking psychogenetic studies, Piaget established that organisms are not passive achievers of knowledge or reactors to external conditions; to the contrary, the system seeks its own experience and reacts to stimuli with active and creative changes in itself and in the environment. Piaget's genetic epistemology gave a plausible explanation for the relation between cognition and action (as the Santiago School of Maturana and Varela put it: no cognition without action, and no action without cognition). Piaget emphasized the emergence of cognitive abilities out of a groundwork of sensorimotor abilities. At the beginning of an interaction there is no *subject* and no *object*. Both result from the internal organization of the subject's experience with the external. For Piaget, boundaries between the cognitive subject and the outside object were not *given* qualities but *created* categories of the world. The cognitive system was the subject-environment unity. Piaget attempted to show the constructivist-interactionist power between the two antagonistic mechanisms of life: organization and adaptation - maintenance and change - essential for every natural process, like development, evolution, and cognition. Development, in this view, is the construction of all kinds of causal factors—genetic, epigenetic, ecological, social and cultural factors—which interact together in a self-organized and not centrally controlled manner (Stotz, 1996). His understanding of ontogenesis hugely influenced his conception of evolution. Piaget was one of the first to take a developmental perspective on evolutionary processes. His genetic epistemology was a biology of knowledge based on an evolutionary theory situated between the extremes of (neo-) Darwinism and Lamarckism. Behavior is seen as a driving force in evolution, and an adaptation to the environment is understood as the result of an interactive construction of self and the environment.

Before going through the main tenets of evolutionary theory, variation, heredity, selection and adaptation, and the role the active organism is playing in all of them, we first have to address the very preconditions for biological evolution. Organisms as they exist today may owe their existence to evolution, but the evolutionary process in turn crucially depends on the existence of living systems that exhibit the necessary preconditions, namely the capacity to (a) produce variation (variability), (b) transmit information for the reconstruction of the life cycle to the next generation (heritability), and (c) adapt the behavior to the contingencies of the environment (adaptability). In summary, populations of organisms must exhibit the ability to evolve, the production of heritable variation in fitness, i.e., differential reproductive success (evolvability). These preconditions, if fulfilled, produce natural selection. Organisms are not just actively engaged in the business of being alive—"acting on their own behalf" (Kauffman, 2000), they are at the same time creating the pre-conditions for evolution, and actively shape the evolutionary process.

There are two main ways they do so: the developing organism can modify the selection pressure acting on the population via the processes of niche construction (Odling-Smee et al., 2003) and cultural evolution (Boyd and Richerson, 1985); or the developmental system can actively create evolutionary novelties and variation, since new variations are the raw material of evolution. For Piaget the "central problem remains": is the environment through its influence on development and behavior "also a causal factor in the actual formation of morphological characteristics" (Piaget, 1978, p. xi)? The extended evolutionary synthesis entails the belief that "the environment not only selects variation, it helps construct variation" (Gilbert and Epel, 2009, p. 369). Hence, the second way to shape the evolutionary process is by creating different and interacting channels of heredity with varying degree of reliability and adaptive plasticity that help to recreate and modify the life cycles of the next generations.

The hypothesis of molecular epigenesis, which could only be sketched here in a rough outline but is substantiated by 20 years of experimental research, very strongly supports the developmental plasticity exhibited by almost all organisms in a more or less extensive degree. Hence the developmental process, during which the organism is in a very tight relationship to its developmental environment, is potentially a very important contributor to heritable variation.

Recent theories in cognitive science have begun to focus on the active role of organisms in exploring and shaping their own environment, and the role of these environmental resources for cognition. Within cognitive science, with its long history of interpreting the mind as a disembodied symbol-processing machine, 4E cognition has been treated as quite a radical departure. Approaches such as situated, enacted, embodied, embedded, ecological, distributed and particularly extended cognition look beyond "what is inside your head" to the old Gibsonian question of "what your head is inside of" and with which it forms a wider whole—its internal and external cognitive niche. Similar embodied and extended views have been proposed within (philosophy of) biology, most notably Developmental Systems Theory and the theories of (selective) and developmental niche construction.

These two views are sometimes seen as mere analogies to each other. From the view of embodied and enacted cognition, in particular, this should immediately be seen as a mistake. The developmental construction intimately relates to the construction of cognition, since biological brains are the control systems for biological bodies. Cognition is the organism's permanent interaction with the world. Even more so in organisms with complicated brains while interacting with the world they permanently construe this world, which in turn influences its impact on development. The mind can only be understood in the context of its relationship to a physical body, which allows it to interact with the world. This world in turn is part of the biological and cognitive system. The body or the mind alone is often not a meaningful unit of analysis because of the dense and continuous information flow between mind, body and world.

The relationship between an active developing system with exploring cognitive abilities and its capacity to construct its own living environment—and that for its descendents—becomes immediately obvious. Since the organism-environment relationship creates selection pressures that will have an important feedback on the phenotype of future generations, the organism indirectly and partially controls its own evolution. This argument has been extensively developed and defended by Odling-Smee, Laland and Feldman (e.g., 2003). The important role of niche construction and scaffolded or extended cognition particularly for human evolution has also been widely argued for (e.g., Sterelny, 2003, 2010; Wheeler and Clark, 2008). But the relationship of the active organism, embedded in its environment, and developmental plasticity to create evolutionary variation and innovations crucially depends on its ability to make these modifications heritable.

Only quite recently did new mechanisms come to light that showed to what extent heredity is indeed a developmental achievement, as the embryologists of the nineteenth century have argued. First, epigenetic mechanisms inherited through the germline made the idea more palatable to biologists, for whom any transmission outside the germ line was previously principally excluded from consideration. There were earlier hypotheses, notably genetic assimilation and accommodation, that that afforded explanation seemingly Lamarckian phenomena by genetic inheritance, widely construed. But since inheritance has now been somewhat detached from its dogmatic relationship with the genetic system, it becomes possible to interpret other transgenerational transmissions as inherited. Parental effects have long been recognized as a main contributor to the offspring phenotype. This phenotype develops out of contributions received from the parents (both genetically and behaviorally) and environmental contributions. Why should some of these trans-generationally transmitted resources not be accepted as contributing to the inheritance of the offspring, as long as they influence the dynamics of evolution?

But all of these exogenetic contributions of inheritance rely critically on the active organism embedded in its own niche, namely caring for its offspring (like the nutritional contribution to the egg, the positioning of the seeds, and parental care in birds and mammals), and the organism's complex relationship with its offspring that actively co-construct the offspring's developmental niche. Epigenetic, behavioral, ecological, and epistemic inheritance depends on the environment experienced and provided by the parent.

This paper couldn't possibly focus on all aspects of an extended evolutionary synthesis and has chosen the, from the author's perspective, most important but also most highly debated aspect, namely non-genetic inheritance. Within this area the paper has barely touched cultural inheritance because most papers on extended inheritance and its importance particularly for human development and evolution has focused on that. Instead it stressed particularly those aspects of extended inheritance that lie between genetic and cultural inheritance, the still gray area of epigenetic and behavioral inheritance systems that play a role in parental effects. These are the processes that can be regarded as transgenerational developmental plasticity and that I think can most fruitfully contribute to, and be investigated by, an extended evolutionary psychology.

ACKNOWLEDGMENTS

I want to thank two blind reviewers and particularly the editor Danielle Sulikowski for many helpful comments. This project/publication was made possible through the support of an Australian Research Council's Discovery Projects (project number 0878650), and a grant from the Templeton World Charity Foundation: Causal Foundations of Biological Information TWCF0063/AB37. The opinions expressed in this publication are those of the author and do not necessarily reflect the views of the Templeton World Charity Foundation.

REFERENCES

Alberts, J. R. (2008). The nature of nurturant niches in ontogeny. *Philos. Psychol.* 21, 295–303. doi: 10.1080/09515080802169814

Alberts, J. R., and Schank, J. C. (2006). "Constructing ontogenetic niches," in *Artificial Life X: Proceedings of the Tenth International Conference on the Simulation and Synthesis of Living Systems*, eds L. M. Rocha, L. S. Yaeger, M. A. Bedau, D. Floreano, R. L. Goldstone, and A. Vespignani (Cambridge, MA: MIT Press; Bradford books), 155–156.

Badyaev, A. V., and Uller, T. (2009). Parental effects in ecology and evolution: mechanisms, processes, and implications. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 364, 1169–1177. doi: 10.1098/rstb.2008.0302

Barrett, L., Pollet, T. V., and Stulp, G. (2014). From computers to cultivation: reconceptualizing evolutionary psychology. *Front. Psychol.* 5:867. doi: 10.3389/fpsyg.2014.00867

Bateson, P., and Gluckman, P. D. (2011). *Plasticity, Robustness, Development and Evolution*. Cambridge: Cambridge University Press.

Bjorklund, D. F. (2006). Mother knows best: epigenetic inheritance, maternal effects, and the evolution of human intelligence. *Dev. Rev.* 26, 213–242. doi: 10.1016/j.dr.2006.02.007

Bonasio, R., Tu, S., and Reinberg, D. (2010). Molcecular signals of epigenetic states. *Science* 330, 612–616. doi: 10.1126/science.1191078

Bonduriansky, R. (2012). Rethinking heredity, again. *Trends Ecol. Evol.* 27, 330–336. doi: 10.1016/j.tree.2012.02.003

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

Cacioppo, J. T., Berntson, G. G., Adolphs, R., Carter, S. C., Davidson, R. J., McClintock, M. K., et al. (2002). *Foundations in Social Neuroscience*. Cambridge, MA: The MIT Press.

Champagne, F. A., and Curley, J. P. (2009). Epigenetic mechanisms mediating the long-term effects of maternal care on development. *Neurosci. Biobehav. Rev.* 33, 593–600. doi: 10.1016/j.neubiorev.2007.10.009

Cosmides, L., and Tooby, J. (1997). *Evolutionary Psychology: a Primer*. Available online at: http://www.cep.ucsb.edu/primer.html

Craig, L. R. (2010). The so-called extended synthesis and population genetics. *Biol. Theory* 5, 117–123. doi: 10.1162/BIOT_a_00035

Crick, F. H. C. (1958). On protein synthesis. *Symp. Soc. Exp. Biol.* 12, 138–163.

Danchin, É., Charmantier, A., Champagne, F. A., Mesoudi, A., Pujol, B., and Blanchet, S. (2011). Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nat. Rev. Genet.* 12, 475–486. doi: 10.1038/nrg3028

Davidson, E., and Levine, M. (2005). Gene regulatory networks. *Proc. Natl. Acad. Sci. U.S.A.* 102, 4935. doi: 10.1073/pnas.0502024102

Donald, M. (2000a). "The central role of culture in cognitive evolution: a reflection on the myth of the "isolated mind"," in *Culture, Thought and Development*, eds L. Nucci, G. B. Saxe, and E. Turiel (Mahwah, NJ: Lawrence Erlbaum Associates), 19–38.

Donald, M. (2000b). *Cognitive Evolution and the Definition of Human Nature*. Little Rock, AR: Morris Foundation.

Geary, D. C., and Bjorklund, D. F. (2000). Evolutionary developmental psychology. *Child Dev.* 71, 57–65. doi: 10.1111/1467-8624.00118

Gilbert, S., and Epel, D. (2009). *Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution*. Sunderland, MA: Sinauer Associates.

Gilbert, S. F. (2003). "The reactive genome," in *Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology,* eds G. B. Müller and S. A. Newman (Cambridge, MA: The MIT Press), 87–101.

Gissis, S. B., and Jablonka, E. (2011). *Transformations of Lamarckism: from Subtle Fluids to Molecular Biology*. Cambridge, MA: The MIT Press.

Gottlieb, G. (2001). "A developmental psychobiological systems view: early formulation and current status," in *Cycles of Contingency: Developmental Systems and*

Evolution, eds S. Oyama, P. E. Griffiths, and R. D. Gray (Cambridge, MA: MIT Press), 41–54.

Griffiths, P. E., and Gray, R. D. (1994). Developmental systems and evolutionary explanation. *J. Philos.* 91, 277–304. doi: 10.2307/2940982

Griffiths, P. E., and Stotz, K. (2000). How the mind grows: a developmental perspective on the biology of cognition. *Synthese* 122, 29–51. doi: 10.1023/A:1005215909498

Griffiths, P. E., and Stotz, K. (2013). *Genetics and Philosophy: an Introduction*. Cambridge: Cambridge University Press.

Hall, B. K. (1999). *Evolutionary Developmental Biology*, *2nd Edn.* Dortrecht: Kluwer.

Hall, B. K. (2011). "A brief history of the term and concept of Epigenetics," in *Epigenetics: Linking Genotype and Phenotype in Develoment and Evolution,* eds B. Hallgrimsson and B. K. Hall (Berkeley, CA:University of California Press), 9–13.

Hallgrimsson, B., and Hall, B. K. (2011). "Introduction," in *Epigenetics: Linking Genotype and Phenotype in Develoment and Evolution,* eds B. Hallgrimsson and B. K. Hall (Berkeley, CA: University of California Press), 1–5.

Holliday, R. (2006). Epigenetics: a historical overview. *Epigenetics* 1, 76–80. doi: 10.4161/epi.1.2.2762

Jablonka, E., and Lamb, M. J. (1995). *Epigenetic Inheritance and Evolution: the Lamarkian Dimension.* Oxford: Oxford University Press.

Jablonka, E., and Lamb, M. J. (2005). *Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life*. Cambridge, MA: The MIT Press.

Jablonka, E., and Raz, G. (2009). Transgenerational epigenetic inheritance: prevalence, mechanisms, and implications for the study of heredity and evolution. *Q. Rev. Biol.* 84, 131–176. doi: 10.1086/598822

Kauffman, S. A. (1969). Metabolic stability and epigenesis in randomly constructed genetic nets. *J. Theor. Biol.* 22, 434–467. doi: 10.1016/0022-5193(69)90015-0

Kauffman, S. A. (2000). *Investigations*. Oxford; New York: Oxford University Press.

Kirschner, M. W., and Gerhart, J. C. (2010). "Facilitated variation," in *Evolution: The Extended Synthesis,* eds G. B. Mueller and M. Pigliucci (Cambridge, MA: The MIT Press), 253–280.

Kuryatov, A., Laube, B., Betz, H., and Kuhse, J. (1994). Mutational analysis of the glycine-binding site of the NMDA receptor: structural similarity with bacterial amino acid-binding proteins. *Neuron* 12, 1291–1300. doi: 10.1016/0896-6273(94)90445-6

Lamm, E., and Jablonka, E. (2008). The nurture of nature: hereditary plasticity in evolution. *Philos. Psychol.* 21, 305–319. doi: 10.1080/09515080802170093

Lehrman, D. S. (1970). "Semantic & conceptual issues in the nature-nurture problem," in *Development & Evolution of Behaviour,* ed D. S. Lehrman (San Francisco, CA: W. H. Freeman and co), 17–52.

Maestripieri, D., and Mateo, J. M. (2009). *Maternal Effects in Mammals*. Chicago, IL: The University of Chicago Press.

McGonigle, B. O., and Chalmers, M. (2008). Putting Descartes before the horse (again!). Commentary on Penn, D., Povinelli, D.J and Holyoak, K. *J. Behav. Brain Sci.* 31, 142–143. doi: 10.1017/S0140525X08003683

Meaney, M. J. (2001). Maternal care, gene expression, and the transmission of individual differences in stress reactivity across generations. *Annu. Rev. Neurosci.* 24, 1161–1192. doi: 10.1146/annurev.neuro.24.1.1161

Meaney, M. J., and Szyf, M. (2005). Environmental programming of stress responses through DNA methylation: life at the interface between a dynamic environment and a fixed genome. *Dialogues Clin. Neurosci.* 7, 103–123.

Menary, R. (2010). Introduction to the special issue on 4E cognition. *Phenomenol. Cogn. Sci.* 9, 459–463. doi: 10.1007/s11097-010-9187-6

Michel, G. F., and Moore, C. L. (1995). *Developmental Psychobiology: an Interdisciplinary Science.* Cambridge, MA: MIT Press.

Moore, C. L. (2003). Differences between organism-environment systems conceived by Lehrman and Gibson: what's in the nest of reciprocities matters. *Dev. Psychobiol.* 42, 349–356. doi: 10.1002/dev.10108

Mousseau, T. A., and Fox, C. W. (1998). *Maternal Effects as Adaptations*. Oxford: Oxford University Press.

Odling-Smee, F. J., Laland, K. N., and Feldman, M. W. (2003). *Niche Construction: the Neglected Process in Evolution*. Princeton, NJ: Princeton University Press.

Oyama, S. (1999). "The nurturing of natures," in *On Human Nature. Anthropological, Biological and Philosophical Foundations,* eds A. Grunwald, M. Gutmann, and E. M. Neumann-Held (New York, NY: Springer), 163–170.

Oyama, S., Griffiths, P. E., and Gray, R. D. (eds.). (2001). "Introduction: what is developmental systems theory?," in *Cycles of Contingency: Developmental Systems and Evolution* (Cambridge, MA: MIT Press).

Piaget, J. (1970). *Genetic Epistemology*. New York, NY: W. W. Norton and Company.

Piaget, J. (1978). *Behavior and Evolution*. Transl. by Nicholson-Smith. New York, NY: Pantheon Books.

Pigliucci, M. (2007). Do we need an extended evolutionary Synthesis? *Rev. Evol.* 61, 2743–2749. doi: 10.1111/j.1558-5646.2007.00246.x

Pigliucci, M. (2009). An extended synthesis for evolutionay biology. *Ann. N.Y. Acad. Sci.* 1168, 218–228. doi: 10.1111/j.1749-6632.2009.04578.x

Pigliucci, M., and Kaplan, J. (2006). *Making Sense of Evolution: the Conceptual Foundations of Evolutionary Biology*. Chicago; London: University of Chicago Press.

Pigliucci, M., and Müller, G. B. (2010). "Elements of an extended evolutionary synthesis," in *Evolution: The Extended Synthesis,* eds M. Pigliucci and G. B. Müller (Cambridge, MA: The MIT Press), 3–17.

Ptashne, M., and Gann, A. (2002). *Genes and Signals*. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.

Sarkar, S. (1996). "Biological information: a sceptical look at some central dogmas of molecular biology," in *The Philosophy and History of Molecular Biology: New Perspectives,* ed S. Sarkar (Dordrecht: Kluwer Academic Publishers), 187–232.

Schneirla, T. C. (1957). "The concept of development in comparative psychology," in *The concept of development,* ed D. B. Harris (Minneapolis, MN: University of Minnesota Press), 78–108.

Sterelny, K. (2003). *Thought in a Hostile World: The Evolution of Human Cognition*. Oxford: Blackwell.

Sterelny, K. (2010). Minds: extended or scaffolded? *Phenomenol. Cogn. Sci.* 9, 465–481. doi: 10.1007/s11097-010-9174-y

Stotz, K. (1996). The psychology of knowledge in the context of evolutionary theory: reflections on the link between cognition and sociability. *Evol. Cogn.* 2, 22–37.

Stotz, K. (2006a). With genes like that, who needs an environment? Postgenomics' argument for the ontogeny of information. *Philos. Sci.* 73, 905–917. doi: 10.1086/518748

Stotz, K. (2006b). Molecular epigenesis: distributed specificity as a break in the central dogma'. *Hist. Philos. Life Sci.* 28, 527–544.

Stotz, K. (2006c). "Constructing your environment: from developmental systems to extended minds," in *Artificial Life*, eds L. M. Rocha, L. S. Yaeger, M. A. Bedau, D. Floreano, R. L. Goldstone, and A. Vespignani (Cambridge, MA: The MIT Press; Bradford Books), 157–158.

Stotz, K., and Allen, C. (eds.). (2008). *Reconciling nature and nurture in the study of behavior. Philos. Psychol.* 21 (Special Issue).

Stotz, K. (2010). Human nature and cognitive-developmental niche construction. *Phenomenol. Cogn. Sci.* 9, 483–501. doi: 10.1007/s11097-010-9178-7

Stotz, K., and Allen, C. (eds.). (2008). *Reconciling Nature and Nurture in the Study of Behavior, Philosophical Psychology*, 21.

Stotz, K., and Allen, C. (2012). "From cell-surface receptors to higher learning: a whole world of experience," in *Philosophy of Behavioural Biology,* eds K. Plaisance and T. Reydon (Boston, MA: Springer), 85–123. doi: 10.1007/978-94-007-1951-4_5

Tomasello, M. (2000). *The Cultural Origins of Human Cognition*. Cambridge, MA: Harvard University Press (First Paperback Edition).

Uller, T. (2012). "Parental effects in development and evolution," in *The Evolution of Parental Care,* eds N. J. Royle, Per T. Smiseth, and M. Kölliker (Oxford: Oxford University Press), 247–266.

Waddington, C. H. (1953a). Genetic assimilation of an acquired character. *Evolution* 7, 118–126. doi: 10.2307/2405747

Waddington, C. H. (1953b). The "Baldin Effect," "Genetic Assimilation" and "Homeostasis." *Evolution* 7, 386–387. doi: 10.2307/2405346

Wade, M. J. (1998). "The evolutionary genetics of maternal effects," in *Maternal Effects as Adaptations,* eds T. A. Mousseau and C. W. Fox (Oxford: Oxford University Press), 5–21.

West, M. J., and King, A. P. (1987). Settling nature and nurture into an ontogenetic niche. *Dev. Psychobiol.* 20, 549–562. doi: 10.1002/dev.420200508

West, M. J., and King, A. P. (2008). Deconstructing innate illusions: reflections on nature-nurture-niche from an unlikely source. *Philos. Psychol.* 21, 383–395. doi: 10.1080/09515080802200999

West, M. J., King, A. P., and Arberg, A. A. (1988). "The inheritance of niches," in *Handbook of Behavioral Neurobiology: Developmental Psychobiology and Behavioral Ecology*, ed E. M. Blass (New York, NY: Springer), 41–62.

West, M. J., King, A. P., and White, D. J. (2003). The case for developmental ecology. *Anim. Behav.* 66, 617–622. doi: 10.1006/anbe.2003.2221

West-Eberhard, M. J. (2003). *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.

Wheeler, M., and Clark, A. (2008). Culture, embodiment and genes: unravelling the triple helix. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 363, 3563–3575. doi: 10.1098/rstb.2008.0135

Wilkins, A. (2011). Epigenetic inheritance: where does the field stand today? What do we still need to know? in *Transformations of Lamarckism: From Subtle Fluids to Molecular Biology,* eds S. B. Gissis and E. Jablonka (Cambridge, MA: The MIT Press), 389–393. doi: 10.7551/mitpress/9780262015141.003.0040

Youngson, N. A., and Whitelaw, E. (2008). Transgenerational epigenetic effects. *Annu. Rev. Genomics Hum. Genet.* 9, 233–257. doi: 10.1146/annurev.genom.9.081307.164445

Conflict of Interest Statement: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Received: 21 April 2014; accepted: 30 July 2014; published online: 20 August 2014.
*Citation: Stotz K (2014) Extended evolutionary psychology: the importance of transgenerational developmental plasticity. Front. Psychol. **5**:908. doi: 10.3389/fpsyg.2014.00908*
This article was submitted to Evolutionary Psychology and Neuroscience, a section of the journal Frontiers in Psychology.

Advantages of publishing in Frontiers

OPEN ACCESS
Articles are free to read,
for greatest visibility

COLLABORATIVE PEER-REVIEW
Designed to be rigorous
– yet also collaborative,
fair and constructive

FAST PUBLICATION
Average 85 days from
submission to publication
(across all journals)

COPYRIGHT TO AUTHORS
No limit to article
distribution and re-use

TRANSPARENT
Editors and reviewers
acknowledged by name
on published articles

SUPPORT
By our Swiss-based
editorial team

IMPACT METRICS
Advanced metrics
track your article's impact

GLOBAL SPREAD
5'100'000+ monthly
article views
and downloads

LOOP RESEARCH NETWORK
Our network
increases readership
for your article

Frontiers
EPFL Innovation Park, Building I • 1015 Lausanne • Switzerland
Tel +41 21 510 17 00 • Fax +41 21 510 17 01 • info@frontiersin.org
www.frontiersin.org

Find us on