

Exaptation, Adaptation, and Evolutionary Psychology

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Abstract

One of the most well known methodological criticisms of evolutionary psychology is Gould's claim that the program pays too much attention to adaptations, and not enough to exaptations. Almost as well known is the standard rebuttal of that criticism: namely, that the study of exaptations in fact depends on the study of adaptations. However, as I try to show in this paper, it is premature to think that this is where this debate ends. First, the notion of exaptation that is commonly used in this debate is different from the one that Gould and Vrba originally defined. Noting this is particularly important, since, second, the standard reply to Gould's criticism only works if the criticism is framed in terms of the former notion of exaptation, and not the latter. However, third, this ultimately does not change the outcome of the debate much, as evolutionary psychologists can respond to the revamped criticism of their program by claiming that the original notion of exaptation is theoretically and empirically uninteresting. By discussing these issues further, I also seek to determine, more generally, which ways of approaching the adaptationism debate in evolutionary biology are useful, and which not.

Exaptation, Adaptation, and Evolutionary Psychology

I. Introduction

From a methodological point of view, one of the most well known accusations of evolutionary psychology – the research program emphasising the importance of appealing to evolutionary considerations in the study of the mind – is the claim that it is overly “adaptationist” (for versions of this accusation, see e.g. Richardson 2007; Sterelny & Griffiths 1999, 331-332; Gould, 1991, 1997a). In one of its most famous versions, by one of evolutionary psychology’s most famous critics – Stephen Jay Gould – this accusation takes the following, more specific form: evolutionary psychologists assume too quickly and without sufficient argument that most of our cognitive traits are *adaptations*, without considering the possibility that they might be *exaptations* instead (Gould 1991, 1997a, 1997b).

However, ever since it was first formulated, Gould’s criticism has been met with stiff resistance, both by proponents and critics of evolutionary psychology (see e.g. Buller 2005; Andrews et al. 2002; Buss et al. 1998; Dennett 1995, 275-281; Cosmides & Tooby 1992). In particular, a number of researchers have claimed that Gould’s criticism is confused for one reason or another, and that it is therefore unable to show that evolutionary psychology is methodologically flawed in a deep way (see e.g. Pinker 1997b; Buss et al. 1998).

As I try to make clearer in what follows, though, it is in fact the entire discussion here that is beset by confusions – specifically, the way the notion of “exaptation” tends to be used in this discussion is very different from the way the notion has been originally defined by Gould. Because of this, in order to push the debate surrounding the plausibility of evolutionary psychology forwards, it is necessary to clear up these confusions – which is what I am to do in this paper. In particular, I argue for two conclusions here. Firstly, I try to show that the standard

reply to Gould's criticism only works if this criticism is based on the common understanding of "exaptation", and not if it is based on the older, "original" definition of the term. Secondly, though, I also try to show that this only makes for a Pyrrhic victory for Gould, as relying on the older understanding of "exaptation" makes his criticism uninteresting. Bringing this out is relevant not just for the cogency of evolutionary psychology in particular, but also for making clearer which ways of approaching the adaptationism debate in evolutionary biology more generally are useful, and which not.

The paper is structured as follows. In section II, I lay out the ordinary understanding of Gould's criticism, together with the standard reply to it. In section III, I present the original definition of "exaptation" and show that it makes Gould's criticism immune from the standard reply; however, I also show that this novel understanding of Gould's original criticism opens up the possibility of a novel response to the latter. I summarise the discussion and consider its implications for the adaptationism debate in evolutionary biology in section IV.

II. Exaptation, Adaptation, and Evolutionary Psychology – The Standard Reading

In a famous attack on the methodology of evolutionary psychology, Stephen Jay Gould criticised the program for being overly "adaptationist". He claimed that, due to their focus on adaptations, evolutionary psychologists are constantly in danger of overlooking the possibility that many of our cognitive traits might actually be *exaptations* (see especially Gould 1991, 63-64; Gould 1997a, 1997b, 1997c; see also Buss et al. 1998, 540; Andrews et al. 2002, 499).¹ In this section, I

¹ Note that there is also reason to think that Gould objects to the idea of there being parts of the minds that could be selected for independently from other parts of the mind. However, I ignore this criticism in the present context, as it is not directly pertinent to the issues under discussion (for more on this, see e.g. Gould & Lewontin 1979; Dupre 2002; Buller 2005, 84-86; Schulz 2008).

first make this criticism – as it is standardly understood – more precise, and then present and assess the standard reply that has been given to it on that basis.

1. *Gould's Criticism – The Standard Reading*

In order to lay out the standard reading of Gould's criticism most clearly, it is necessary to start by answering two preliminary questions. Firstly, it needs to be made clearer what it means for some trait to be an *adaptation*; secondly, it needs to be made clearer what it means for some trait to be an *exaptation*. I begin with the former.

According to standard usage, "adaptation" is defined as follows (see e.g. Sober 1984; Brandon 1990; Baum & Larsen 1991; West-Eberhard 1992; Sterelny & Griffiths 1999, 218):

(1) T is an adaptation for F if and only if T got selected for doing F.

Two things are important to note about this definition. Firstly, according to it, *adaptation* is a purely historical notion: it describes why a trait (first) spread in a given population, and does not make any claims about whether or not the trait confers current utility to its bearers – i.e. it does not say whether this trait is adaptive now.² Secondly and trivially, the definition makes clear that classifying something as an adaptation is saying that the trait evolved primarily by natural selection: adaptations for F are traits that evolved due to the fact that they conferred fitness advantages to their bearers through bringing about F in the past.

² Note that (Reeve & Sherman 1993) and (Gould & Vrba 1982) use this term slightly differently: the former (ostensibly) only require T to have current adaptive importance for F, and the latter *add* this requirement to (1) (see also Griffiths 1992; Sober 2008, chap. 3.11). However, for now, it is best to stick to the standard, purely historical meaning; I return to these issues at the end of the paper.

The second preliminary point that needs to be addressed concerns the definition of “exaptation”. Unlike in the case of “adaptation”, though, the issues here get fairly complex fairly quickly. In particular, as I try to make clearer in what follows, there is a major disconnect in how the notion of an *exaptation* was originally defined and how it is commonly used and understood. To avoid confusion, I therefore proceed in two steps. Firstly (in this section), I define “exaptation” in a way that is consistent with how the notion is normally employed in the discussions surrounding evolutionary psychology. Given this, I then return (in the next section) to the way the notion has been originally defined by (Gould & Vrba 1982), and see to what extent this changes the conclusions derived in this section.

With this in mind, note that “exaptation” is usually understood as follows (see e.g. West-Eberhard 1992; Dennett 1995, 275, 279, 281, 390; Buss et al. 1998, 539; Sterelny & Griffiths 1999, 219; Andrews et al. 2002, 491, 500-501; Buller 2005, 84):

- (2) T is an exaptation if and only if T is now adaptive for F, and
- (a) T was selected for F' (where F and F' are different), or
 - (b) T is a by-product of a different adaptation T'.

Three points are useful to note about this definition.

Firstly, as defined in (2), *exaptation* is not just a historical notion. Of course, classifying something as an exaptation does make a historical claim about why the trait spread in a given population: it either was itself selected for (though for a different reason from what it is currently adaptive for) or it is the by-product of a different trait that was selected for. However, an

exaptationist claim in the sense of (2) also says something about contemporary features of the trait – it is now adaptive.

Secondly, note that this notion of *exaptation* is still “anchored” in natural selection (Buss et al., 1998, 542-543, 546; Andrews et al. 2002, 491). In particular, as in the case of an adaptation, the trait in question still is assumed to be the product of natural selection – either directly (as in (2)(a)), or indirectly, by being linked to other traits which spread by natural selection (as in (2)(b)). This focus on natural selection is important, as it means that the definitions in (1) and (2) are not exhaustive of the space of evolutionary possibilities: in particular, there are (adaptive) traits that are neither adaptations nor exaptations – for example, traits that evolved purely by drift or migration. This will become important again below.

Thirdly, note that traits that are by-products of other adaptations (i.e. part (2)(b) of the above definition) are sometimes called “spandrels” (Gould & Lewontin 1979; Cronin 1991, 93; Gould 1991, 1997a, 1997b; Buller 2005, 84; Richardson 2007, 55). It is useful to be very explicit about this, as the terminology of “spandrel” is almost as controversial as that of “exaptation” (see e.g. Dennett 1995, 267-282; Pinker 1997b; Gould 1997b, 1997c; Buss et al. 1998, 539; Andrews et al. 2002, 491). It is important to note, therefore, that “spandrel” is always used here to refer to the subset of exaptations characterised by (2)(b).

With definitions (1) and (2) in the background, two possible interpretations of Gould’s criticism of evolutionary psychology can now be laid out more precisely (Gould 1991, 1997a, 1997b, 1997c). Firstly, he could be expressing an *empirical* worry concerning evolutionary psychological research: evolutionary psychologists often accept falsely – or without sufficient evidence – that what explains the spread of some trait T in the population is natural selection for some function F of T, whereas this spread should (or at least reasonably could) either be

explained by the fact that T was selected for some different function F', or by the fact that T is the by-product of some other trait T' that got selected for F. That is, the worry here is that, by only focusing on cognitive adaptations, evolutionary psychologists are led into misclassifying (or at least classifying without sufficient evidence) the evolutionary nature of our cognitive traits.³

Secondly, Gould could be expressing a *methodological* worry concerning evolutionary psychological research: by only investigating what our cognitive adaptations are, evolutionary psychologists prevent themselves from finding out much that is of interest when it comes to the evolutionary history of our minds. Specifically, even if they manage to correctly identify all our cognitive adaptations, they will still be unable to draw up a (near) complete evolutionary picture of our minds, as they are missing out on investigating our cognitive exaptations – a class that is orders of magnitude larger than that of our cognitive adaptations (see e.g. Gould 1997a).⁴

For present purposes, it is only the methodological criticism that is important. The reason for this is that the empirical worry is just that – empirical. In order to address it, what is necessary is an extended inquiry of the research done to date by various evolutionary psychologists, to see whether and how often they have misclassified the evolutionary aspects of our cognitive traits. Put differently: the issues surrounding the empirical worry are straightforward factual ones – they do not raise concerns with evolutionary psychology as a research program, but merely point to the possibility that particular evolutionary psychologists have accepted false selectionist hypotheses. While it might not be straightforward to determine whether this is so, it is in principle clear what needs to be done – and the outcome of this sort of inquiry does not have any

³ Alternatively (or additionally), one might say that evolutionary psychologists are wrong about – or fail to provide sufficient evidence for – the (evolutionary) function or character they ascribe to various cognitive traits.

⁴ Alternatively (or additionally), one might say that, by being based on adaptations only, the discovery heuristics evolutionary psychologists rely on are overly constrained, so that the latter are unable to discover many novel cognitive traits, or many novel functions of known cognitive traits (see also Machery forthcoming; Grantham & Nichols 1999; Davies 1999). I thank two anonymous referees for useful discussion of this point.

immediate implications for evolutionary psychology in general (see also Buss et al. 1998, 543-545; Andrews et al. 2002; Pinker 1997b; Gould 1997a, 1997b).⁵

This, though, is different in the case of the methodological criticism. There, the concern is precisely with the methodology of evolutionary psychology *in general*: the claim is that, even if done correctly (i.e. without misclassifying the evolutionary history of any of our cognitive traits), evolutionary psychology is constrained in an important way, as it cannot investigate our cognitive exaptations. That is, even if evolutionary psychologists were right about all of their particular conclusions, their program overall would not be vindicated, as it would be overly limited in extent – it would leave out of consideration much that it should consider. Note that, at least on the face of it, this is indeed an important and powerful criticism of evolutionary psychology: it goes beyond claiming that mistakes in the pursuit of the program have been made – it argues that the program is inherently and strongly limited in what it can achieve. It is therefore no wonder that evolutionary psychologists have been very forceful in responding to this criticism, and that they have spent much time and energy in doing so: in particular, key researchers in the area have published several lengthy papers in major journals solely to rebut this charge (see Pinker 1997b; Buss et al. 1998; Andrews et al. 2002; see also Stump 2010).⁶ Determining whether this criticism gets at something important is far from straightforward, however; investigating this is the aim of the rest of this paper.

⁵ Of course, this does not mean that it is not important for evolutionary psychologists to address this worry (see also below).

⁶ The exaptationist criticism of evolutionary psychology gains even further importance due to the fact that Gould has had a lot of “visibility” in the public sphere – indeed, he published this charge (among other places) in non-specialist journals (see Gould 1997a, 1997b). Hence, this charge deserves to be taken seriously also due to the fact that it calls into question the “scientific credentials” of evolutionary psychology in the eyes of policy makers and the wider public. I thank Cecilia Heyes for useful remarks about this point.

2. *The Standard Reply to Gould's Criticism*

Unsurprisingly, Gould's methodological attack on evolutionary psychology has been subjected to heavy critical scrutiny, and a number of responses have been formulated to it, both by proponents and critics of evolutionary psychology (see e.g. Buller 2005, 84-86; Andrews et al. 2002 and their respondents; Buss et al. 1998; Dennett 1995, 267-282). While these responses differ in numerous particulars, it is possible to distil a common core out of them; in what follows, I shall call this common core the "standard reply" to Gould's criticism.⁷

This standard reply begins by noting that exaptations are still the product of natural selection: whether the origin of the trait is as in (2)(a) or (2)(b), it remains the case that, ultimately, an exaptation depends on the workings of natural selection. This matters, as it makes clear that investigating adaptations is in fact a necessary part of the investigation of exaptations: the identification of the adaptations of an organism must be the *key step* in the identification of its exaptations. Put differently: there is no other way for evolutionary psychologists to proceed in finding out about whether parts of our minds are exaptations than to find out about our cognitive adaptations first – we can only identify the former after we have identified the latter (see e.g. Andrews et al. 2002; Buller 2005, 84-86). This is so, as, on the one hand, in order to say that T is an exaptation in the sense of (2)(a), we need to say what T first got selected for (i.e. what it is an adaptation for); at the very least, we need to establish that it is an adaptation for some F' that is different from what T is currently adaptive for. On the other hand, in order to say that T is a spandrel, we need to say what other trait T is a by-product of – as by-products can only be

⁷ For the sake of argument, I here grant Gould's point that it is in fact true that evolutionary psychologists do not take into account exaptations in the sense of (2) in their investigations of the mind. However, there is reason to think that this is somewhat misleading: (Pinker 1997a), for example, claims that some parts of our minds – e.g. our taste for music and art – are only (adaptive) by-products of other parts of our minds (e.g. our ability to recognise safe and resource-rich environments); (Symons 1979), too, reasons in this manner.

specified in terms of their “base”. Hence, there is no reason to think that the focus on adaptations is as methodologically constraining as alleged by Gould.

Now, at this point, it may be objected that none of this invalidates Gould’s claim that evolutionary psychologists need to do more than identifying adaptations: concentrating on the latter just is not enough to provide a compelling evolutionary approach to (human) psychology. In other words, it may be true that identifying our adaptations is a *necessary* part of the determination of cognitive exaptations – but it is not a *sufficient* one. In particular, one still needs to determine whether the trait in question is currently adaptive for a reason that matches the one that it was first selected for, and whether this trait is not just a by-product of some other cognitive adaptation (see also Preston 1998). Finding out about the relevant adaptations is not all there is to the determination of our cognitive exaptations – more needs to be done here. Hence, the fact that the investigation of exaptations depends on the investigation of adaptations does not make the former any less important – and Gould’s criticisms stands.

However, for two reasons, this objection cannot fully block the standard reply to Gould’s criticism. Firstly, it seems plausible that, at least in many cases, identifying adaptations is in fact sufficient for finding out about exaptations (Buss et al. 1998, 537; Andrews et al. 2002, 541; Rutherford 2002; Thompson 2002). This is so, as, on the one hand, establishing that some trait got selected for F often puts one in a position to also establish that this trait is now adaptive for some different F’ (West-Eberhard 1992, 14). For example, assume we have good reason to believe that certain aesthetics dispositions – e.g. to find certain landscapes visually appealing – can be adaptive *both* for enabling humans to be successful hunter-gatherers *and* for enabling them to be successful farmers (this might be due to the fact that what makes a landscape good camping ground might also make it good farm land). Assume also that we have good reason to

believe that these aesthetic dispositions were indeed selected for in the Pleistocene (when humans were hunter-gatherers), and that, in the recent past, many humans switched to subsistence farming. Given this, one can conclude that these aesthetic dispositions must now be exaptations for many humans: to the extent that human lifestyles have changed from hunting and gathering to farming, these dispositions will now have changed function as well.

On the other hand, establishing that some trait T got selected for F often also tells one about the by-products of T. In particular, since investigating an organism's adaptations often requires considering the genetic, ontogenetic, and environmental co-determinants of that trait, one is frequently put in a position to also find out about traits that are linked to this trait (Buss et al. 1998, 537, 546; Gould 1997b; West-Eberhard 1992). For example, the knowledge that humans originally evolved a disposition to quickly and reliably recognise safe and resource-rich camping grounds, together with information about how human visual and emotional cognition works in general, might lead one to conclude that fictional representations of certain environments – as opposed to actual environments – will now be found emotionally attractive, and therefore be sought out and created.⁸

Secondly, even when this is not the case – so that establishing what our cognitive adaptations are really is not sufficient for establishing what our cognitive exaptations are – this still does not fully revive the fortunes of Gould's criticism. The lack of sufficiency merely points to the fact that we need to find out *more* about our cognitive adaptations. This, though, may easily be accepted as true by evolutionary psychologists – it hardly points to a major flaw in the methodology of their research program. Of course, we want to find out as much as we can about our cognitive adaptations – including whether they are adaptive now (and if so, why) and what

⁸ For more on this example, see e.g. (Pinker 1997a).

their by-products are.⁹ However, this in no way invalidates evolutionary psychology's focus on assembling a list of our cognitive adaptations *first*: evolutionary psychologists have to start somewhere, and reminding them that they should not stop their investigations too soon is not making a major criticism of their methodology – it is a fundamental endorsement of their project (see also Dennett 1998).

In a nutshell, therefore, the standard reply to Gould's criticism notes that, far from being misguided, evolutionary psychologists' focus on adaptations is in fact a necessary (and maybe even a sufficient) part of the investigation into our cognitive exaptations. By assembling a list of all our adaptive cognitive adaptations, we are putting up the scaffold around which the list of our cognitive exaptations can be erected. In other words, it is not clear why we should think that evolutionary psychologists are precluded from investigating our cognitive exaptations by their focus on adaptations. Hence, Gould is wrong in faulting the methodology of evolutionary psychology for focusing too much on adaptations: given his interest in investigating exaptations, he should in fact *applaud* this focus (see especially Andrews et al. 2002). However, as the next section aims to make clearer, this dialectical situation changes quite dramatically once we recognise that Gould's criticism could also be seen to be based on a different notion of exaptation.

III. Exaptation, Adaptation, and Evolutionary Psychology – An Alternative Reading

There is good reason not to rest content with the above refutation of Gould's criticism. As I suggested earlier and will spell out in more detail in what follows, it turns out that the definition of the notion of *exaptation* is not fully unambiguous. Given the fact that Gould's criticism rests

⁹ Evolutionary psychologists might also respond that it is not clear that investigating the current adaptive value of a cognitive trait is either feasible or part of their project (see e.g. Buss et al. 1998). See also below.

crucially on this notion, it therefore seems clear that it would be premature to conclude that the above standard reply settles all the issues in this context. Rather, it seems more reasonable to ask what happens to the dialectic here if, instead of relying on the common definition of “exaptation” (i.e. (2) above), Gould’s criticism is built on the original definition of this notion (as laid out in Gould & Vrba 1982).

Answering this question is the aim of this section. In particular, I show that Gould’s methodological criticism can in fact be made immune from the standard reply by having it rest on the original definition of “exaptation”. However, given this, I then go on to show that doing so raises a different set of problems – and that this set of problems once again makes this criticism implausible. Consider these two steps in turn.

1. *Gould’s Criticism – The Non-Standard Reading*

When first introduced in 1982, “exaptations” were defined in the following disjunctive manner: “a character, previously shaped by natural selection for a particular function (an adaptation), is coopted for a new use”; or “a character whose origin cannot be ascribed to the direct action of natural selection (a nonadaptation), is coopted for a current use” (Gould & Vrba 1982, table 1 and p. 5–6; see also Gould 1991, 48, 54–55; Griffiths 1996, 524). Expressed more formally and concisely, this can be put as follows::

(3) T is an exaptation if and only if T is adaptive for F now, but has evolved for reasons other than selection for F in the past.

Two points are usefully noted about this definition.

Firstly, like the “exaptation” of (2), the “exaptation” of (3) is not merely a historical notion. Specifically, like (2), definition (3) makes a claim about the current adaptive value of T *and* about the evolutionary history of T. However, unlike (2), the historical claim made by (3) is a purely negative one: classifying T as an exaptation does not express why T spread in the relevant population, but merely expresses why it did *not* do so. As will be made clearer in a moment, this negativity is very important to the status of Gould’s criticism; however, for now, it can just be as accepted as it stands.¹⁰

Secondly, note that natural selection plays no special role in (3), even though it is the foundation of (2). Specifically, while an exaptation in the sense of (3) still *might* depend on natural selection (as long as it was for a reason other than bringing about F), it *need not*: the trait in question could instead have spread by (a combination of) drift, migration, cultural evolution, or any other evolutionary determinant (either directly or indirectly, through being a by-product of a trait that has spread in this way). Unlike (2), therefore, definition (3) of “exaptation” is not anchored in natural selection in any particular way, but allows T to have spread for reasons that have nothing to do with this evolutionary determinant at all.

These differences between (2) and (3) are important for two reasons. On the one hand, they are frequently conflated. This is problematic, as it creates much confusion in the debate surrounding exaptations, and makes many of the arguments given in this context hard to follow or even fallacious. For example, after citing definition (3), Buller says:

¹⁰ As made clear by (Gould & Vrba 1982), the notion of *exaptation* was also meant to be a theoretically cogent replacement of the confused, teleological notion of *preadaptation* that had some currency in the history of evolutionary biological thought. Whether or not such a replacement was needed, though, is still an open question. See also below.

[A]s this definition entails, there are two kinds of exaptations. One kind is a co-opted adaptation [...]. The other kind of exaptation is [...] a developmental by-product of an adaptation. (Buller 2005, 84)

Unfortunately, as noted earlier, this is *not* what definition (3) entails – though it *is* (trivially) entailed by definition (2). Equally, Buss et al. refer to definition (3), and then say:

In sum, Gould [...] proposed two types of functional exaptations – adaptations that initially arose through natural selection and were subsequently co-opted for another function [...] and features that did not arise as adaptations through natural selection but rather as side effects of adaptive processes [...]. (Buss et al. 1998, 539)

Again, this is true for definition (2), but not for definition (3).¹¹ For clarity's sake alone, therefore, it is important to disentangle the two definitions.

On the other hand, noting that (2) and (3) are different is important, as the standard reply to Gould's criticism only works against the version of this criticism based on (2), not against that based on (3). The key point to note in this context is that, given (3), the notions of adaptation and exaptation are structurally not connected to each other in any particularly deep way. In particular, as noted above, saying that T is an exaptation in the sense of (3) does not commit one to seeing it as having spread by natural selection *in any way*. Because of this, there is now no reason to think

¹¹ The discussion in (Buss et al. 1998) is actually multiply confusing, since the authors further say that Gould also “seemed to use the term to cover novel but functionless uses or consequences of existing characteristics” (Buss et al. 1998, 539). This is confusing, in that this is not an alternative definition of “exaptation” used by Gould at all – spandrels are part of both the (2) and (3) readings of the notion. Put differently, the issue here is not whether exaptations need to be assumed to have *functions* (be adaptations themselves), but whether they need to be seen to be somehow tethered to some adaptation or other.

that every exaptation must, in principle, be describable in terms of some adaptation – the (1) and (3) notions of “adaptation” and “exaptation” are logically completely independent from each other. Realising this is crucial, as it implies that it is no longer possible for defenders of evolutionary psychology to claim that focusing on adaptations is at least necessary, and maybe even sufficient, for investigating exaptations. Put differently, given sense (3) of “exaptation”, a list of our cognitive adaptations might have little to do with a list of our cognitive exaptations – the two lists can feature traits that are evolutionarily completely independent from each other.¹² In particular, exaptations that are the result of non-selective factors like drift and cultural evolution (or which are by-products of traits shaped by these processes) will not feature on a list of adaptations and their by-products – and would thus be overlooked by evolutionary psychologists.

What this makes clear is that, with (3) in the background, Gould’s criticism stands: by focusing on adaptations, evolutionary psychologists are forced to overlook the possibility that many of our cognitive traits might be exaptations – the investigation of the latter calls for a completely different approach than the investigation of the former. Note that this is a principled point about the basic structure of evolutionary psychological methodology – it may of course happen to be the case that all of our cognitive exaptations have been adaptations first (i.e. that they are all exaptations in the sense of (2)). The point made here, though, is that this would then be a matter of luck. In general, there is no reason to think that by focusing on our cognitive adaptations, we are getting anywhere close to assembling a list of our cognitive exaptations in the sense of (3). Hence, evolutionary psychologists are still in need of a response to this worry – at least on the face of it, they can still be accused of being too limited in their methodological

¹² Of course, the two lists might overlap for contingent reasons. The point made here, though, is just that this overlap is not something one can rely on for principled reasons. See also below.

toolbox. However, as the next sub-section aims to make clear, such a response can in fact be given.

2. *A Novel Reply – The Unimportance of Exaptations Per Se*

Despite the fact that Gould's criticism, in the "novel" reading just presented, overcomes the standard reply to it, there is still reason to think that it will ultimately remain unconvincing. In the main, this is because it is not at all clear that it can give plausible support to the claim that the inability of evolutionary psychologists to investigate our cognitive exaptations – as defined in (3) – really is a major problem.

To see this, begin by noting that what *would be* interesting and important to point out is that evolutionary psychologists pay insufficient attention to the selection / non-selection distinction – i.e. the fact that there is more to evolution than natural selection (for some recent work on this distinction, see e.g. Godfrey-Smith 2001; 2009; Richardson 2007; Andrews et al. 2002, 498; Orzack & Sober 1994; Beatty 1992). In other words, if the core of Gould's attack is the claim that evolutionary psychologists are only looking for traits that have been selected for, when many of our cognitive features have evolved for other reasons, then that will certainly make for a major criticism of the program. Furthermore, there is no doubt that this claim is something that Gould in fact does subscribe to and argue for (sometimes in the same publications as cited earlier – not to mention in Gould & Lewontin 1979).

The trouble is that, if this is all that Gould is trying to say, then his message is being obscured by being phrased in terms of the notion of an *exaptation*. To see this, note that, given definition (3), the notion of *exaptation* cuts across the selection / non-selection distinction: for example, it is entirely possible to investigate exaptations by only considering selectionist hypotheses (e.g. by

merely considering traits that have been selected for one reason, and are now adaptive for another); equally, one can investigate non-selectionist hypotheses without considering any exaptations at all (e.g. by merely investigating traits that are not now adaptive). Because of this, if Gould is seen as merely being concerned with pointing out that evolutionary psychologists ought to consider non-selectionist hypotheses more frequently, his emphasis on the importance of exaptations becomes highly obscure.

Importantly, the same goes for the claim that Gould merely wants to point out that evolutionary psychologists and other (alleged) adaptationists confuse current adaptive value with the reason for the trait's existence. This, too, is an issue that has nothing to do with exaptations as such – for example, an adaptation that no longer has any adaptive value is not an exaptation in the sense of either (2) or (3) – and is nowadays simply marked by the distinction between being adaptive and being an adaptation (Sober 1984; Sterelny & Griffiths 1999, 217-220; Stump 2010). Given this, one may wonder what other argument Gould could be trying to make here. What reason is there for why evolutionary psychologists ought to take exaptations in the sense of (3) more seriously than they have so far? Alas, the answer to this question appears to be “none”. This is for three reasons.

Firstly, the class of our cognitive exaptations in the sense of (3) is vast, especially when compared to that of our cognitive adaptations (this is even admitted by Gould himself: Gould 1991, 58-59; Gould 1997a); moreover, most members of this class are utterly trivial and uninteresting.¹³ Since current environments are drastically different from past environments (partly due to changes we have initiated ourselves – Odling-Smee et al. 2003; Sterelny 2012), a large number of our adaptive cognitive traits are likely to have spread for reasons other than

¹³ (Browne 2002, 545) also notes that the class of exaptations is large and predominantly uninteresting; however, he argues for this in the context of (Andrews et al. 2002) – which rests on the (2) sense of exaptation.

having been selected for what they are currently adaptive for – the relevant environmental circumstances are simply too recent in origin to assume anything else. For example, it is quite plausible that the ability to deal with complex financial instruments is an exaptation: this ability is plausibly adaptive now (at least in many cultures), but complex financial instruments have not been around for long enough to have led biological evolution to build specific cognitive tools for dealing with them. Importantly also, establishing this truth about our cognitive abilities is not something that greatly deepens our understanding of our minds – in fact, it is something that can be derived largely from the armchair, and merely adds to our (immense) amount of uninteresting knowledge about the way we think and act.

The second reason for doubting the importance of exaptationist hypotheses of type (3) is that the historical claim established by these hypotheses is purely negative: all we learn is how some cognitive trait did *not* evolve. However, such purely negative historical claims are not very interesting: what we ultimately want to know is how our minds *did* evolve – not how they did not evolve. This, though, is beyond the remit of an exaptationist investigation in the vein of (3). In particular, the latter ends with the refutation of a particular hypothesis (i.e. that trait T initially evolved by having been selected for F), but does not go on to the positive establishment of how the relevant trait did, in fact, evolve.¹⁴ It thus ends before the interesting part of the investigation has begun.¹⁵

¹⁴ It is useful to note that this differs from sense (2) of “exaptation”. There, establishing which parts of our minds are exaptations was interesting – for it told us something about how the different parts of our minds actually came about. Knowing that some adaptive cognitive trait changed its function over time in a specific way, or that it is merely a by-product of some adaptation, tells us much about this trait – in particular, it tells us about how this trait spread. However, in the case of (3), finding out about the fact that some trait is an exaptation will, in and of itself, not tell us much about the evolutionary history of this trait at all: it just tells about one way it did not spread.

¹⁵ Of course, establishing an exaptationist claim of type (3) is interesting if it allows evolutionary psychologists to rule out one of the major hypotheses under consideration in a certain area. For example, if it is a hotly debated question whether a part of our mind (e.g. our logical reasoning abilities) evolved for one specific reason (e.g. cheating detection) or another (e.g. domain-general inference making), then finding out that it did *not* evolve for one of these reasons (which moreover is adaptive) *is* interesting – it shows that one particular hypothesis in this area is

Thirdly and finally, focusing on the fact that exaptations in sense (3) are not *purely* historical, but establish an evolutionary “switch” in the adaptiveness of a trait (from it not being adaptive to it being adaptive, or from it being adaptive for something other than F to it being adaptive for F), does not help in making this notion particularly interesting either. The reason for this is that these kinds of switches happen all the time: environments change (as noted above, sometimes through the doing of the organism itself: Odling-Smee et al. 2003; Sterelny 2012; Stotz 2010), and it is utterly commonplace that traits become adaptive for something that does not explain their spread in the population. It is thus not clear what we gain by establishing a list of these “switched” cognitive traits (i.e. a list of the traits that experienced some switch or other): it is likely that this list would be both quite long and not very interesting.

The bottom line is this: what we are interested in is establishing how our cognitive traits did arise, not how they did not arise, or merely which of them are adaptive for reasons that do not explain their spread in the population. However, exaptationist reasoning of type (3) can only establish the latter kinds of claims, not the former. Hence, investigating cognitive exaptations in the sense of (3) does not seem to be a very interesting project. For these reasons, it becomes clear that Gould’s exaptationist criticism of evolutionary psychology sounds, at best, like nothing more than an appeal to considering more alternative hypotheses in the investigation of the evolutionary history of our minds. While reminding evolutionary psychologists to consider more alternative hypotheses might certainly be useful, it does not amount to a particular pointed methodological criticism of their research – in fact, evolutionary psychologists would (again)

not an accurate description of the trait’s evolutionary genesis, and that, by elimination, the other one is more likely to be true (see Sober 2008 for more on contrastive reasoning of this kind). However, this does not alter the point in the text, as the value of the exaptationist claim then derives from the fact that the domain of relevant hypotheses had already been narrowed to these two hypotheses – which had to be established beforehand. (Note also that we cannot reason by elimination and enumerate all the true negative historical claims about some trait so as to arrive at the true positive one – there are simply too many of the former to make this a feasible strategy, even in principle.)

seem to be able to simply accept this as a call for more work in their area (see also Dennett 1995, 270-271). In short: Gould's exaptation-based criticism again turns out not to be very compelling – but this time, this is because it is not clear that the inability to investigate cognitive exaptations should be seen as a major problem for evolutionary psychologists.

It is worth stressing again that this does not amount to a defence of evolutionary psychology from the charge of adaptationism more generally – in particular, for all I have said, it might well be the case that this program does not pay sufficient attention to non-selectionist hypotheses, or that the selective hypotheses it considers are too simplistic (e.g. in leaving out the possibility of gene-culture co-evolution, niche construction, and frequent changes in function: see e.g. Richerson & Boyd 2005; Odling-Smee et al 2003; Sterelny 2003). It is also worth stressing again that these are very important issues for evolutionary psychologists to address. The point here is just that Gould's criticism, in so far as it is based on the notion of exaptation, cannot be seen to either make *this* argument well, or another interesting one – there is not another criticism here of evolutionary psychology, besides the ones just mentioned.

IV. Conclusion

To conclude, it is useful to take a brief step away from evolutionary psychology in particular, and note that there is a more general point in the background here, too. The fact that when relying on either definition (2) or (3), the notion of exaptation emerges as not playing an interesting role in evolutionary psychological research suggests that the importance of this notion in evolutionary biology quite generally might be overstated. In particular, the above argument gives reason to think that (Gould & Vrba 1982) might have been mistaken in suggesting that “exaptation” is a “missing term” in evolutionary biology: at the very least, the argument shows

that appealing to “exaptations” is not useful for determining the limits of adaptationist reasoning in science and beyond (see also Dennett 1995, 281; Zuk 2002, 534).¹⁶

This is important to note, as it gives credence to and refines a conclusion that others have reached as well (see e.g. Buss et al. 1998, 542; Dennett 1995; Griffiths 1992, 1996). Ever since the publication of (Gould & Vrba 1982), various researchers in the field have thought that, while providing a corrective for overly strong forms of adaptationism certainly is worthwhile, it is not clear that relying on the notion of exaptation is useful for doing so.¹⁷ The main reason that is typically given for this is that this notion is said to overemphasise the first selection of a trait, and to downplay the importance of later (stabilising, maintaining) selection of it (Brandon 1990, 172; Reeve & Sherman 1993, 3-4; Griffiths 1992, 1996; Sterelny & Griffiths 1999, 218-220; Dennett 1995, 281; Sober 2008, chap. 3.11; see also Stump 2010).¹⁸

In this context, the arguments of this paper matter, as they refine this criticism in two ways. Firstly, they make clear that this criticism does not apply as strongly to understanding (3) of “exaptation” as it does to understanding (2) of the notion: as noted above, Gould & Vrba’s original definition of “exaptation” does not actually say why a trait first spread – it merely notes that it was for reasons other than what it is adaptive for now. While this is still making a somewhat sharp distinction between the first origination of the trait and its later evolution, it is far less sharp than before: in particular, it is now based on only a weak negative claim about this origination (what it was *not* determined by), and does not focus on the first *selection* of a trait at all. This might well take some of the sting out of the common attack on the notion of exaptation.

¹⁶ Alternatively, one might say that the above argument diagnoses the reason for why the uptake of the notion of *exaptation* in the evolutionary biological literature in general has been relatively meager.

¹⁷ For more on adaptationism in general, see especially (Godfrey-Smith 2001).

¹⁸ A slightly more specific version of this worry is the idea that a vast quantity of our traits must have spread for reasons other than what they are currently adaptive for – after all, due to the fact of common ancestry, all life derives from a simple common ancestor, and in many ways has merely changed the function of the latter’s traits (e.g. the structure of its cells, etc.). In turn, this puts the notion of exaptation in danger of being de facto trivial (see e.g. Dennett 1995, 281, for more on this). I thank an anonymous referee for discussion of this point.

Secondly, however, the arguments of this paper also show that switching to the (3) understanding of “exaptation” does not in fact rehabilitate this notion. In particular, the paper makes clear that, even if understanding (3) can be seen to avoid an overemphasis on the first spreading of a trait, it does so at the cost of becoming fairly contentless: saying that a trait is an exaptation is no longer saying much at all about this trait – it merely notes that this trait is one of the many that is adaptive, but for something that does not account for its spread in the relevant population. In short: thinking about exaptations when doing evolutionary biology seems unhelpful either because it is too strongly focused on why a trait first spread in a given population (on the (2) reading) or because it does not say much at all about why a trait spread in a given population (on the (3) reading). Either way, our understanding of the challenges of adaptationist reasoning has not been improved.

In all, therefore, I hope to have shown that Gould’s classic criticism of evolutionary psychology as overlooking the possibility that many of our cognitive traits might be exaptations is unconvincing – and that this is so even if it is refined in such a way that it can overcome the standard reply to it. In particular, if “exaptation” is defined so as to be consistent with the common discussion of the term, the investigation of exaptations in fact depends on the investigation of adaptations. By contrast, if “exaptation” is defined so as to only make a negative historical claim about how a trait did *not* evolve, the notion – and thereby, Gould’s criticism – loses most of its theoretical interest. In short: there are a lot of important issues still to be addressed when it comes to adaptationism in general and evolutionary psychology in particular – however, the lack of the consideration of exaptations should not be seen to be among them.

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