

Stephen J. Gould and Adaptation: San Marco 33 Years Later

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Abstract Stephen J. Gould's concern for the wide variety of explanations for evolutionary change was one of his chief intellectual contributions. In one of his most famous papers, "The Spandrels of San Marco", named in honor of Venice's own most gloried church, and which he co-authored with Richard C. Lewontin, he emphasized the importance of historical, correlational, byproduct, and phyletic evolutionary explanations, and contrasted these with adaptationist explanations. In this Article, I take a more formal approach to discussing Gould's analysis of evolutionary explanations, now 33 years later. My analysis rests on the "logic of research questions", and contrasts a "methodological adaptationist" approach, to what I call the "evolutionary factors" approach. In the former, the key research question is: "What is the function of this trait?" while in the latter, the research question is: "what evolutionary factors account for the form and distribution of this trait?" I use my case study on the evolution of the female orgasm, which Gould defended in his column, and was one of his favorite examples, to illustrate how the methodological adaptationist approach can lead scientists astray. (Reports of a serious challenge to the byproduct account, based on recent poorly-designed twin studies, are unsupported.) Biases induced by methodological adaptationism have led biologists to a failure to compare the byproduct hypothesis against an adaptive one with regard to the evidence. Perhaps, then, it is past time to take Gould's advice, and reevaluate whether methodological adaptationism is truly as benign as it is commonly assumed to be.

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1 Introduction

We do not usually think about the logic of our scientific methods leading to close-mindedness, and the inability to see alternatives, or evaluate evidence, but that's exactly what sometimes happens in evolutionary biology with one of its most popular methods, despite its benign reputation, and true to the warnings given by Stephen Jay Gould and Richard Lewontin 33 years ago in their profoundly influential paper, "The Spandrels of San Marco and the Panglossian Paradigm" (1979).

1.1 Adaptive Explanation

The issues about method revolve around evolutionary adaptations, one of Evolution's biggest successes. Evolutionary adaptations are traits that exist today because they were products of natural selection acting in the past history of the species. Take the timber wolf, one of Darwin's examples. Descended from more generalized and slower carnivores, the wolf evolved specialized traits for hunting swift prey like deer and elk. There was variation in the past of the traits of speed and strength, and because there was a reproductive advantage associated with these traits, and selection for them, we have the wolf's specialized adaptations for speed and strength today. There's an important pattern manifest in the population distribution of speed in this example. In the ancestral population, speed was highly variable, with values representing the different speeds distributed widely over the population, which we can visualize as a very low or squashed bell curve, or even a flat curve. After selection has acted over evolutionary time, we have a large peak in the population distribution of speed, up at high speed. Selection processes normally produce peaks in population distributions of traits, at the value of the trait with the best fit—or closest-to-best fit—to its environment. The wolf example thus presents a good example of a natural selection explanation that produces an adaptation. Our living world is filled with examples of such adaptations.

Now, let us consider a breed of scientist called a 'methodological' or 'heuristic' adaptationist. This is an evolutionary biologist who *assumes*, at the beginning of investigation, that the trait that they are looking at is, indeed, an adaptation. As one of the founders of modern evolutionary theory, Ernst Mayr, memorably wrote, in reaction to the Spandrels paper, and in defense of an adaptationist research program, "The adaptationist question, 'What is the function of a given structure or organ?' has been for centuries the basis for every advance in physiology" (Mayr 1983, p. 153).

While this approach may look biased, since it seems that adaptive explanations would be unfairly favored, this favor is supposed to be only temporary. This more benign methodological adaptationist method has been advocated by many biologists since Mayr, and here is a philosopher's characterization of it:

... when the hypothesis of optimality [or adaptation] is investigated first, deviation from the optimum provides evidence that other factors are at work, and perhaps the nature of the deviation will give clues about where to look next (Godfrey-Smith 2001, p. 342).

This is described as the “most helpful way to proceed”; look for a selective explanation in every case, and it might lead you to nonselective explanations, which you could then pursue if that is where the evidence led. But it is still an open question whether the method *in practice* allows non-adaptive explanations ever to win the day. Do researchers who avow such approaches in fact find themselves willing to embrace non-adaptive explanations when the evidence points toward them?

1.2 *The Spandrels of San Marco and the Logic of Research Questions*

Problems only arise for the methodological adaptationists when a trait appears in a population that is not the direct consequence of natural selection. In Gould and Lewontin’s 1979 paper, they discuss the spandrels of the church of San Marco, which are the triangular areas between the arches holding up the dome, and onto which saints have been painted, and they write that:

... The design is so elaborate, harmonious, and purposeful, that we are tempted to view it as the starting point of any analysis... But this would invert the proper path ... Yet evolutionary biologists, in their tendency to focus exclusively on immediate adaptation to local conditions, do tend to ignore architectural constraints and perform just such an inversion of explanation (Gould and Lewontin 1979, pp. 79–82).

In their paper, Gould and Lewontin emphasize a basic fact of evolution, namely, that not every biological character is adaptive, and that there exist alternative evolutionary explanations available and sometimes appropriate, such as evolutionary developmental accounts, architectural byproduct accounts, accounts that cite correlations of growth, and so on. But they emphasize that there is an important difference between paying lip service to this view, and using this theoretical assumption in actual research.

Now, later in history, we are in a position to see a clear contrast between two distinct methodologies and corresponding sets of questions. And we know that different questions make different answers legitimate. I call this the ‘Logic of Research Questions’. The logic of the research question we ask constrains what type of answers we can give, so we need to think very hard about the research questions we ask, because the questions can lead us to actually miss what’s really going on, and therefore to scientific failure.

The methodological adaptationist asks, echoing Mayr’s rebuttal to Gould and Lewontin, “what is the function of this trait?” And there are any number of possible answers to this question, which take the form:

Possible Answers:

A: The function of this trait is B

A: The function of this trait is C

Etc.

I characterize an alternative approach here, as the ‘evolutionary factors’ approach, whose research question is: “What evolutionary factors account for the form and distribution of this trait?” And it has a series of possible answers, including:

Possible Answers:

A: This trait occurs in the population because it has the function B, which is an adaptation

A: This trait occurs widely in this population because it is genetically linked to a trait that is highly adaptive in this species

A: This trait has its current form largely because of an ancestral developmental pattern.

Etc.

Note that the first answer is an adaptation answer, which suggests that adaptation is also explored, as a priority, in the evolutionary factors approach.

2 Case Study: The Evolution of the Female Orgasm

Let us turn to a case study in the logic of research questions—it is a provocative and interesting case study, but please do not lose sight of the fact that it is only a case study, and not itself the point of the paper.

I use my case study on the Evolution of the female orgasm, which Gould wrote about and defended in his column in *Natural History* magazine—in fact, it was one of his favorite examples of an evolutionary developmental byproduct—to illustrate and confirm how the methodological adaptationist approach can lead scientists astray (Gould 1987).

I should say at the start that reports of the demise of the byproduct account of female orgasm are greatly exaggerated. A recent twin study by Zietsch and Santtila claimed to have undermined the byproduct account (2011). They first said that the byproduct account predicted that what they called “orgasmic function” should be correlated in male and female twins. But their twin study showed that it was not correlated. The chief and fatal problem with the study is that the traits studied under the name “orgasmic function” were hopelessly different: they counted the time to orgasm in men, that is, the time it takes for a man to have orgasm once he starts copulation, and compared it to a completely different measure in women, whether or not she has orgasm at all (2011, p. 1098). As you can see, these two traits are quite distinct, and would not be expected to correlate, in any case. Thus,

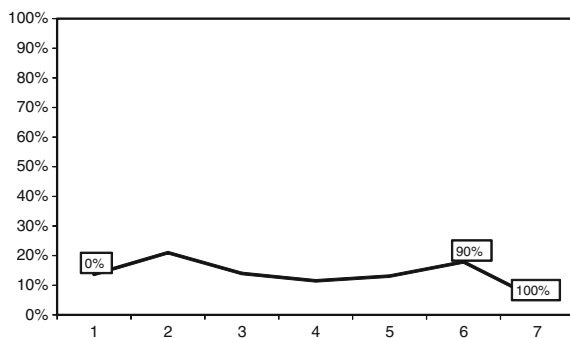
the lack of correlation of these two traits that Zietsch and Santtila found was to be expected, and says nothing against the byproduct view, contrary to their claim (2011, p. 1100; Wallen et al. 2012).

In my book published in 2005, *The Case of the Female Orgasm*, and quickly translated into Italian (2006), I gave detailed examinations of all 21 published theories of how female orgasm had evolved; 20 of them claimed that orgasm was an evolutionary adaptation. With the wolf case, we saw an important kind of evidence that is at stake when evolutionists consider an adaptive account of a trait. That is, directional selection produces a peak somewhere in the distribution of the trait in the population; the same is true of stabilizing selection, the type of selection (on males) involved in the byproduct account. Now contrast the peak at high speed in the population distribution of wolves with the distribution we find of orgasmic performance among women (Fig. 1).

Note that only about 13 % of women always have orgasm from intercourse, and roughly a third of women rarely or never have orgasm with intercourse in their whole lives. In Dawood et al.'s data, 13 % of women never have orgasm at all from any means (2005). These data are consistent with the results from the 35 studies I analyze in my book (2005), and also a more recent, large twin study (Dunn et al. 2005). As you can see, this curve is basically flat. Simple selective forces produce peaks in the distribution curves of a trait, as more and more of the organisms in a population are selected to have the desirable form of the trait. All except one of the proposed selective explanations for female orgasm predicts a peak in this curve, but there are no peaks. Hence, all but one of the selective and adaptive explanations for female orgasm is undermined by these data from sexology.

There is another way in which all of the adaptive explanations, including the Female choice theory, are undermined by sexology data, as well. Zietsch and colleagues (2011) examined correlations of such potentially adaptive traits and orgasmic activity in a population of nearly 3,000 women, finding zero to very weak correlations across all 19 traits they examined including libido, social class, orientation toward uncommitted sex, restrictive attitudes towards sex, lifetime number of sex partners, and so on. None of the correlations had significant genetic

Fig. 1 The x-axis represents overall orgasmic performance with heterosexual vaginal intercourse, while the y-axis represents frequency in the population. Constructed from Dawood et al. (2005)



components, thus undercutting any ascription of a fitness benefit to orgasm. In addition, there has never been any evidence linking orgasm to fitness or number of babies, frequency of intercourse, or any other trait correlated to fitness, and this new study echoes this very significant lack (Bancroft 1989). In other words, having orgasms is not associated with having more or better babies, the very basis of selective change.

2.1 The Fantastico Bonus Account (Aka Byproduct Account)

Now, I would like you to consider the problem of why male mammals have nipples. Nipples clearly provide a reproductive advantage to female mammals by providing the means to feed the offspring; they have an evolutionary function. But there is no known contribution to fitness, or function, for the males.

The evolutionary explanation for the existence of male nipples is a non-adaptive one in the males, based on the development of the embryo. Males and females share the same embryological form at the beginnings of life; they start off with the same basic body plan, and only if the (chromosomally male) embryos receive a heavy dose of hormones during the 8th week of pregnancy do any sexually distinguishing characteristics appear. In females, nipples are adaptations—they were actively selected for—but the males get them for free. This sort of explanation is a ‘developmental’ or ‘non-adaptive’ one—male nipples are seen as evolutionary byproducts, with no function of their own.

A parallel explanation was offered, by anthropologist Donald Symons, back in 1979, for the female orgasm. Females have orgasm because orgasm is strongly selected in males, and both sexes share the common form in the womb. The tissues involved in orgasm for males and females are homologues, including nerve tissues, erectile tissues, and muscle fibers. Thus, females get the orgasmic tissues through this embryological connection and are often capable of having orgasms under the right conditions of rhythmic stimulation.

There is a variety of evidence supporting this byproduct account of female orgasm, although it has encountered a great deal of resistance. Part of this is surely the “byproduct” name, which many women find demeaning. So I’m in the process of renaming it the “fantastico bonus” account, which is much more accurate, after all.

Symons’s account accords well with the data available about human female sexuality. Women do not masturbate by simulating intercourse, that is, solely by vaginal insertion, they do it by stimulating the clitoris directly or indirectly (Kinsey et al. 1953). Men masturbate the same way, by stimulating the homologous organ.

Ten of the adaptive accounts assume that women virtually automatically have orgasm with intercourse, the way men do, and when faced with the real sex evidence, they cannot account for the lack of orgasmic frequency (Lloyd 2005). The byproduct theory, though, allows us to make sense of the infrequency with which women experience orgasm with reproductive sex.

Symons's general thesis is also supported by the nonhuman primate evidence, which shows, among other things, that female stump-tail macaques have the distinctive contractions and other bodily markers characteristic of orgasm.

Note that Symons and I are not denying that the *clitoris*, as an organ of sensation, almost certainly has been selected because it aids the female in sexual excitement and induces and prepares her to seek out and have intercourse. But this reasoning does not extend to the use of these same tissues for female orgasm. Orgasm is a special reflex that sometimes results from clitoral and genital excitement. Now it is time to consider the female choice type of sexual selection hypothesis, which is the only adaptive hypothesis on offer compatible with the wide variability of orgasmic experience in women, which shows up as the flat curve of orgasmic distribution.

2.2 Female Choice Hypothesis and the Uterine Upsuck Account

The basic idea of the female choice hypothesis offered for female orgasm is that the female will mate with more than one male over either a short period of time, or over different cycles, and have orgasm preferentially with the higher-quality males. These theorists assume that orgasm is accompanied by a mechanism of uterine upsuck that makes it more likely that the female will be fertilized by the higher quality male. Thus, the orgasmic women are required to respond with orgasms only sometimes with intercourse—yes with high quality males, and no with lower quality males (Thornhill et al. 1995; Hosken 2008; Puts et al. 2012). This type of female choice selection can theoretically produce the flat curve of wide orgasm variation, but only provided that the force of selection is strong. Specifically, note that Hosken (2008) appeals to the population genetics models of Pomiankowski and Møller (1995) to produce wide variation, and those models require strong selection. Thornhill et al. (1995) and Puts et al. (2012) produce no selection dynamics with their account, but something like the available female choice genetic models would be required to produce the present variation.

But consider what is needed to fulfill this female choice model. It requires multiple mating by women before insemination. How many women fulfill this in a given population, and how strong a selection pressure can this be, also given that selection on one sex is only half as strong as selection on both? The fitness effect in the selection scenario proposed depends on indirect selection on female orgasm arising from a difference in offspring quality, not quantity, given the opportunity to choose by multiple mating. All this is extremely unlikely to add up to the strong sexual selection required, in order to explain the very high level of phenotypic variation of orgasm. But now there is a new challenge to this model.

In a new study published by neurophysiologist Kim Wallen and I (2011; see Fig. 2), those women who reported orgasm with intercourse (white bars) had

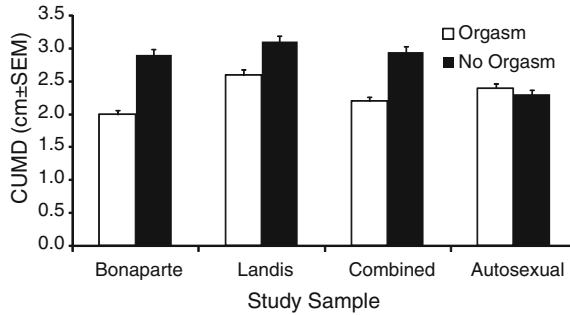


Fig. 2 Average Clitoral-Urinary-Meatus-Distance (CUMD) measurements in the Landis and Bonaparte samples, for those women routinely experiencing orgasm in intercourse (66 % of the time or more, *white bars*) and those not (*black bars*). Data are shown for the samples combined, and for the Bonaparte sample's masturbatory (autosexual) orgasms, as well. Data are all statistically significant, except for the difference in the two autosexual samples

significantly shorter distances between their clitoris and their urinary opening, which appears in Fig. 2 as CUMD, than did women who did not report orgasm with intercourse (black bars). We found this strong correlation in two distinct datasets, Bonapart and Landis, and the difference was highly statistically significant—over two standard deviations, with an r of 0.6 in the combined dataset. We also found that this anatomical distance was strongly *predictive* of whether a woman had orgasm with intercourse. This distance is irrelevant to orgasm with masturbation, as we would expect.

In other words, we found that an anatomical trait, basically this distance between the clitoris and a structure near the vagina, strongly predicted whether or not a woman would have orgasm with intercourse or not. If you think about it, this makes good sense. The further away the clitoris is from the vagina, the less likely it is that she will have an orgasm with intercourse, possibly because her clitoris is not being stimulated enough by the activities going on around the vagina. Clearly, if her anatomy so strongly influences whether or not she has an orgasm with intercourse with a male, that leaves little room for the genetic quality of the male to also strongly influence the outcome of such intercourse. Again, according to the theorists, the selection pressure of this type of selection scenario needs to be quite strong in order to produce any result in terms of evolution. Puts et al. (2012) characterize the anatomical trait and relation we discovered as an aspect of the environment in which female choice evolved, but it seems that our strong correlations make such a scenario quite unlikely.

Overlooking for now the substantial hurdles embodied by this evidence, female choice theory can only work if there is a physiological relation between female orgasm and fecundity, a mechanism that is usually simply assumed. The hypothesis had achieved widespread acceptance since the nineties through the work of Robin Baker and Mark Bellis. But examine their data. In one data set, they have 1 out of 11 couples in the sample contributing 93 out of the 127 data points (nearly three

quarters of the data). 4 of the other 10 couples contributed one data point each, a combined total of 3 % of the data, and so on (Baker and Bellis 1993; see Lloyd (2005) for much more analysis of problems with their statistics). But extrapolating to the population at large based primarily on the results of a single subject badly violates standard statistical practice. In the end, the Baker and Bellis data are statistically worthless and no scientific conclusions can be drawn from them.

But many dozens and even hundreds of adaptationists nevertheless used this paper to support their desired conclusion that female orgasm was an adaptation, and used it directly against the viability of the byproduct account, despite its obvious flaws (e.g., Alcock 1998). The human evolution field's instant acceptance of the Baker and Bellis paper, and its continuing use of the paper in lectures and teaching, as well as research, was an example of adaptationist bias getting the better of scientific judgment or the application of normal statistical standards. Adaptationist bias consists in favoring adaptive accounts over the nonadaptive accounts without good evidence for doing so, or, indeed, against the evidence.

Nowadays, the favorite mechanism for the preferential movement of sperm of the superior male is the effects of oxytocin (Puts et al. 2012). But those experiments used a dose of 400 times the actual level released during orgasm, and are thus irrelevant to the biological question without further research (Levin 2011). So both theoretically and empirically, the female choice hypothesis is facing very substantial hurdles before it could be accepted as a plausible theory of female orgasm. The byproduct hypothesis, on the other hand, has much evidence supporting it. So how are the two evaluated and compared by biologists? Here's where the biases, and above all, methods, really play a central role.

3 Analysis of Methodological Adaptationist Approach Versus Evolutionary Factors Approach

When a methodological adaptationist does research, and asks their key question, "what is the function of female orgasm?", the assumption is that selection brought the orgasmic structures to their present state; the problem or challenge is to figure out which selective hypothesis is correct. So far, we have:

Possible Answers:

A: The function of this trait is to cement the pair bond

A: The function of this trait is to aid in preferential insemination by high-quality males.

But where does the byproduct hypothesis belong? Some of the adaptationists in this case see the byproduct view as a sort of "null" hypothesis. In general usage in science or biology, a null hypothesis is usually a negative alternative to a positive correlational hypothesis. The positive hypothesis would be one in which a trait was positively correlated with fitness or some component of fitness, while a null

hypothesis would be simply the non-correlation with fitness, indicating non-selection. So, on this characterization, the answer would be:

A: The trait is a byproduct of selection on males, and has *no function* in females.

They often call this a “null” result.

For a methodological adaptationist, the non-selective hypothesis is often treated as the failure to find an explanation, which they view as akin to scientific surrender (Alcock 1987, 1998; Sherman 1989). It’s not seen as a positive explanation—in fact, the byproduct explanation is seen as no explanation at all. This is at least partly because it cannot be an answer to our adaptive question, it is *nonresponsive*.

On leading animal behaviorists John Alcock’s and Paul Sherman’s analysis, the byproduct hypothesis is a null result, and offers only a “proximate” explanation of how women come to have orgasms. In other words, it explains how female babies grow up to have orgasms as adult women, but does not offer an evolutionary account. But Alcock writes that

If we were to discover the female orgasm occurred with positive effects on female reproductive success, we would gain an *evolutionary* dimension to our understanding of this trait that is not covered by *any* proximate explanation (emphasis mine, emphasis his, Alcock 1998, p. 330).

Thus, the byproduct account is not seen as an evolutionary account at all—it is not an answer to any evolutionary question about female orgasm, with its own supporting evidence and theoretical standing. Alcock and Sherman treat it as a failure of *evolutionary* explanation altogether. And this is clearly a result of the fact that the only answer to their adaptation question had to do with describing a function for female orgasm. With no reproductive function, the orgasm is seen as having no evolutionary role at all. This is a consequence of the logic of the research question.

Similarly, David Barash, the author of the most widely selling textbook on sociobiology for a couple of decades, and a grandfather of the field of human evolution, writes, with his wife, regarding the impetus behind those favoring the byproduct theory, that it involves

a scientifically legitimate desire to explore all possible explanations for any biological enigma of this sort, including the ‘null hypothesis’ that it might not be a direct product of *evolution* after all (Barash and Lipton 2009, p. 133; my emphasis).

And here, note the equivalence of evolution with selection in this statement; the byproduct explanation is mistakenly not considered evolutionary, just as we saw before with Alcock and Sherman.

So here we have the situation: we ask the Methodological Adaptationist Question:

“what is the function of the female orgasm?” And we consider and test the appropriate answers.

Possible Answers:

A: The function of this trait is B

A: The function of this trait is C

Etc.

But with too many failures, we get what they call the “null” result: That the trait has no function in females. They conclude “it may not be a direct product of evolution at all.” We should correct this answer to: “it may not be a direct product of selection at all.” So, the byproduct answer seems to be, for them:

A: null result: the trait has no known function or correlation with fitness, and may not be a direct product of selection at all.

But we should consider the positive alternative:

A: The trait is a byproduct of selection on males, and has no function in females.

Note that in both cases, there is *no function* in females, which is *still nonresponsive* to the research question of the methodological adaptationists, because it requests a function. Instead, Symons’ byproduct explanation should be seen in terms of the logic of the evolutionary factors research question, specifically, “what evolutionary factors account for the form and distribution of the trait of female orgasm?”

Possible answer:

A: This trait has its current form and distribution largely because it is a byproduct of strong stabilizing selection on the male orgasm. (This is the correct reading of the byproduct theory, a positive alternative causal hypothesis.)

Contrast this answer with the characterization of the byproduct view offered under the methodological adaptationist research method:

Possible answer:

A: This trait has no known function or correlation with fitness, and may not be a direct product of selection at all (what adaptationists call the “null” hypothesis, which they think is equal to the byproduct hypothesis).

Hence, the methodological adaptationists’ portrayal of the byproduct hypothesis is misleading, and in fact, incorrect. When the byproduct hypothesis is treated as merely a non-answer to the adaptive evolutionary question asked, it also cannot be seen as accumulating evidence in its favor. As an answer to the more inclusive evolutionary factors question, the byproduct account is an alternate causal hypothesis to an adaptive account, with a set of specific evolutionary mechanisms involving indirect selection, which can accumulate evidence in its favor: it is not merely a null result. Thus, even though the methodological adaptationists present their adherence to their research program and its attendant question as perfectly harmless and in fact very good and productive science, we can see here, exactly, where it goes astray.

In essence, the byproduct hypothesis *cannot* be an answer to the function question, while it is a perfectly acceptable answer to the evolutionary factors question. We can see in these various researchers' responses to the orgasm case how confused they become by focusing only on their primary research question. For example, when a group of adaptationists were launching arguments against Gould's presentation of Symons's byproduct hypothesis that was based on my analysis, they—very strangely—behaved as if no empirical evidence had been considered at all. Adaptationist Donald Dewsbury, a very distinguished psychologist studying animal reproductive behavior, for example, claimed in response to Gould's discussions that

... we need to study the consequences of orgasm for differential reproductive success and then determine whether a plausible case can be made for drawing the loop from present consequences to the past history of natural selection. These need to be studied, *not asserted or denied a priori* (Dewsbury 1992, p. 103; my emphasis).

The perception was, clearly, that no good evidence had entered into the debate, despite Symons's entire chapter in 1979 detailing evidence supporting his theory, and Gould's appeals to the 66 years of sexology evidence, and so on. But since all of that evidence seemed to favor the byproduct view, a theory that was considered only a null account, it was invisible to these researchers. This is where the logic of research questions really does its damage.

Gould and Lewontin complained in their spandrels paper that if one selectionist explanation failed to explain the trait under investigation, the adaptationists would simply turn to another adaptationist explanation, and then another and another; there seemed no end of selection hypotheses that could be appealed to. In essence, there is no stopping rule for the research question, "what is the function of this trait?" As a result, the lack of evidence favoring all the hypotheses proposed so far for a trait is rightly perceived as no impediment for its future success as an adaptation of some sort; thus, the so-called "null" hypothesis, or no-function view of the byproduct hypothesis is neither attractive nor needed, since a new function story is always available. Note that the repeated failure of adaptationist accounts does not have any bearing on the positive evidence available supporting the byproduct account, although many adaptationists incorrectly believe that this is the sole evidence supporting the account (e.g. Alcock 1998; Lindquist 2006). Because the logic of the function question demands a function answer, no byproduct answer can be considered a positive answer to the research question, and thus have support in its favor, and we do find the participants in the debates following this logic.

On the logic of research questions, though, the evolutionary factors approach works very differently from the methodological adaptationist one in terms of how to treat evidence: an adaptive hypothesis can be compared directly to a non-adaptive, byproduct theory, by comparing evidence in favor of each view. As we saw, under the function question, the byproduct account gets incorrectly classified as a null hypothesis, and a null hypothesis cannot have independent evidence in its favor. But the methodological adaptationists never get a chance to compare the byproduct hypothesis as a positive causal hypothesis because they have no

stopping rule, and would have to give up on their quest for a functional hypothesis, at least temporarily, and switch questions to the evolutionary factors approach. No researcher opposed to the byproduct account involved in this debate has ever done this, at least in print. Compare the two questions and their samples of relevant well-formed answers here:

What is the function of this trait?

Possible Answers:

A: The function of this trait is B

A: The function of this trait is C

A: The function of this trait is D, or E, F...Z, AA, BB,...ZZ, AAA, BBB...???

[Faulty A: This trait has no known function or correlation with fitness, and may not be a direct product of selection at all (what adaptationists call the “null” hypothesis, which they think, falsely, is equal to the byproduct hypothesis)]

Etc.

What evolutionary factors account for the form and distribution of this trait?

Possible Answers:

A: This trait occurs in the population because it has the function B, which is an adaptation

A: This trait has its current form and distribution among one sex largely because it is a byproduct of selection on the opposite sex’s trait

A: This trait occurs widely in this population because it is genetically linked to a trait that is highly adaptive in this species

A: This trait has its current form largely because of an ancestral developmental pattern.

Etc.

Under the logic of research questions, then, those using the methodological adaptationist approach cannot adequately evaluate the accumulated evidence for the byproduct approach. This evidence is in some sense only visible on the evolutionary factors approach, where the weight of evidence is the right rule to use in evaluating the byproduct hypothesis and its alternatives.

The methodological adaptationists also make basic scientific errors arising from their method. For example, several adaptationists repeatedly complain that under the byproduct hypothesis, female orgasm would fade away and deteriorate over evolutionary time, and would tend to disappear from the population. This notion has been advanced not only by leading scientists such as Alcock, Sherman, and Barash, but also by outstanding primatologist and human evolutionist Sarah Blaffer Hrdy, and it is based on a misunderstanding of how the byproduct account works (Alcock 1998; Sherman 1989; Smith 2005). This misunderstanding is likely a consequence of their adaptationist bias that a particular trait will only be sustained in a population if it itself is under sustained selective pressure. But under the byproduct account, the basic muscle, nerve, and tissue pathways involved in female orgasm would be maintained in the female over the generations in virtue of

the fact that they are under ongoing strong selection in the male. Thus, methodological adaptationist explanatory biases have led to fundamental mischaracterizations of the byproduct hypothesis.

4 Conclusions

In conclusion, Gould's approach to evolutionary biology says that we should not privilege adaptation explanations automatically above other alternatives, such as developmental or phyletic ones, and our research methods should not bias our research outcomes. This is among the main messages of Gould and Lewontin's famous spandrels paper, which most biologists say is now passé, and claim that biologists simply do not make those mistakes any more, if they ever did. This is clearly false, as we can see from this problematic case. Even in the most recent discussions in the orgasm controversy, the philosophical, theoretical and evidential issues are unresolved. And I would like to emphasize that I am not in any way against adaptationist explanations themselves. In fact, I think that the first type of explanations that should be considered using the evolutionary factors approach are adaptationist ones; we should start our examination of any trait by asking whether it is adaptive. But I am using this case to highlight some *risks* of a particular approach to research into evolutionary causes. These risks become obvious when we examine the logic of the research questions and their relevant answers, within the methodological adaptationist approach. When a research method makes any particular types of hypothesis especially difficult to entertain or accept, it deserves serious scrutiny. The presence of researchers like Symons who engaged in their research using the more inclusive evolutionary factors approach exemplify an available alternative method. Evolutionists all say that they have learned their lessons about an inclusive approach to evolutionary explanation from Gould and Lewontin's 1979 spandrels article, but methodological adaptationism seems to make it very difficult for them to act on those lessons. Grazie molto.

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