

# Female Orgasm and the Phallic Constraint Hypothesis: The Consequence of the Byproduct Account.

**Abstract** Whereas Gould & Lewontin (1979) accuse adaptationists of ignoring developmental constraints, it has been claimed that this problem is not intrinsic to adaptationism, and that adaptationism has improved in this respect since the ‘spandrels’ paper. However, a proper examination of one of the greatest debates over adaptationism, that over female orgasm, does not show this higher standard being put into practice. This paper explores the ‘phallic constraint hypothesis’ implicit in the so-called byproduct account of female orgasm, not as some ‘anti-adaptationist’ ‘explanation’ of female orgasm but rather as a factor in the structure of adaptationist theory. It is argued that the outcome of this hypothesis is far too significant to be ignored and that in doing so (however inadvertently because the by-product account has generally not been proposed *as a constraint*), the adaptationists of this debate conform closer to the portrayal of Gould & Lewontin than to, for example, that of Mayr (1983) or Dawkins (2006a).

**Keywords** Adaptationism, Female Orgasm, Byproduct, Constraint, Development, Gould

## 1. Developmental Constraint in the Landscape of the Adaptationist Debate

The adaptationist debate set off by Gould & Lewontin (1979) has since been addressed by a wealth of systematic and philosophical literature (e.g. Orzack & Sober 2001). However, the ‘Spandrels’ paper has many different aspects (e.g. ‘story telling’ is a clearly distinct issue from rejecting the ‘bauplan’) and these have not all been dealt with equally. The dominant theme of the literature appears to be ‘optimality’ (the very title of Orzack & Sober’s volume is a case in point). In contrast, Gould & Lewontin’s emphasis on ‘developmental constraint’ and the corresponding condemnation of ‘atomisation’ has received surprisingly little

philosophical attention, given its central polemical significance. This paper hopes to show that, while ‘developmental constraint’ may seem to be little more than, for want of less colloquial terms, an old chestnut, it still has plenty to say about contemporary views of evolution.

The adaptationist response to the ‘constraint’ line of argument was amply articulated by the Modern Synthesis hero Ernst Mayr (1983). The basic response involved both one major agreement and one major disagreement about atomisation. The agreement was that atomisation and the disregard of developmental constraint is indeed an extremely misguided practice. The disagreement was that such thinking is not, contrary to Gould & Lewontin, a necessary part of adaptationism. What Gould & Lewontin saw as adaptationism, Mayr saw as merely badly practiced adaptationism, and what Gould & Lewontin saw as the alternative to adaptationism (i.e. respecting constraint), Mayr saw as adaptationism when rightly practiced.

This point of view has been standard among less revolutionarily minded Darwinists. In *The Blind Watchmaker*, Richard Dawkins (2006a) speaks of a certain ‘school of biologists’ who see ‘Darwinism’ as imagining that selection produces the necessary phenotypes irrespective of embryological patterns. This school of biologists can safely be identified with what he elsewhere describes as the “‘genetic constraints’ brigade”, (2006b, p. 307) and the Darwinists, with adaptationists. Speaking in the name of Darwinism, he states that “what we must insist on is that we can’t afford to ignore the constraints on evolution that embryology imposes.” (2006a, p. 311)

The truism that constraints exist has found expression in a certain tradition of joke-telling. The classic example comes from Maynard Smith: “[i]f there were no constraints on what is possible, the best phenotype would live for ever, would be impregnable to predators, would lay eggs at an infinite rate, and so on.” (1978, p. 32) In his discussion cited above,

Dawkins satirizes the idea of a Darwinist with no concept of constraint: “I suppose the real explanation must be that it just wouldn’t pay cows to jump over the moon. And we mustn’t forget the energetic cost of reaching escape velocity.” (2006a, p. 310)

Philosopher Roger Sansom (2003) has taken this point much further. Sansom points out that any conceivable adaptation necessarily takes place against the backdrop of constraints, such that these constraints are an integral part of any adaptive argument. Optimality, he points out, is judged as the optimal design *given* some set of constraints, however implicit they may be. By the same token, there is no constraint that affects an evolutionary trajectory without doing so against a background of selection. Every argument involves both elements, whichever one the attention may be drawn towards. Adaptation and constraint cannot be separated as though one is the cause and the other is not.

The extent to which adaptationists actually pay due attention to developmental constraints in their theories is but one measuring stick in the broader question of how good or bad adaptationist practice really is or has been. In his response to the ‘Spandrels’ paper discussed above, Mayr claimed that the practice of adaptationists was simply not as bad as Gould & Lewontin had made out. He claimed that certain of the examples used to illustrate the problems of adaptationism had been taken from evolutionary literature that was decades old (1983, p. 327). In an article titled ‘Post-Spandrel Adaptationism’, Rose & Lauder (1996) talk about ‘the death of the old adaptationism’, the sort criticised by Gould & Lewontin, and the move toward a ‘new adaptationism’. Their claim is that adaptationism was indeed faulty when ‘spandrels’ was written, but in response has become new and improved. Orzack & Sober give a somewhat more pessimistic perspective. They note a “discrepancy between perception and practice... many of these [self-fashioned pluralist minded] ‘adaptationists’ practice a research program that appears to be consistent only with the idea that natural

selection is the sole important force.” (2001, p. 4) These authors attribute this discrepancy to the scientist’s desire not to appear ‘conceptually narrow’.

A simple issue emerges from this literature: the ‘reform’ of adaptationism. Perhaps it had already been reformed before ‘spandrels’. Perhaps it has been reformed *since* ‘spandrels’. Or perhaps this reformation, to one degree or other, is still waiting to happen. We could debate this in regard to the practice as a whole. But is reform such an open question with regard to the ‘adaptationist’ position on female orgasm? To find out, we now turn to take a closer look at the byproduct account.

## **2. The Structure of the Byproduct Account**

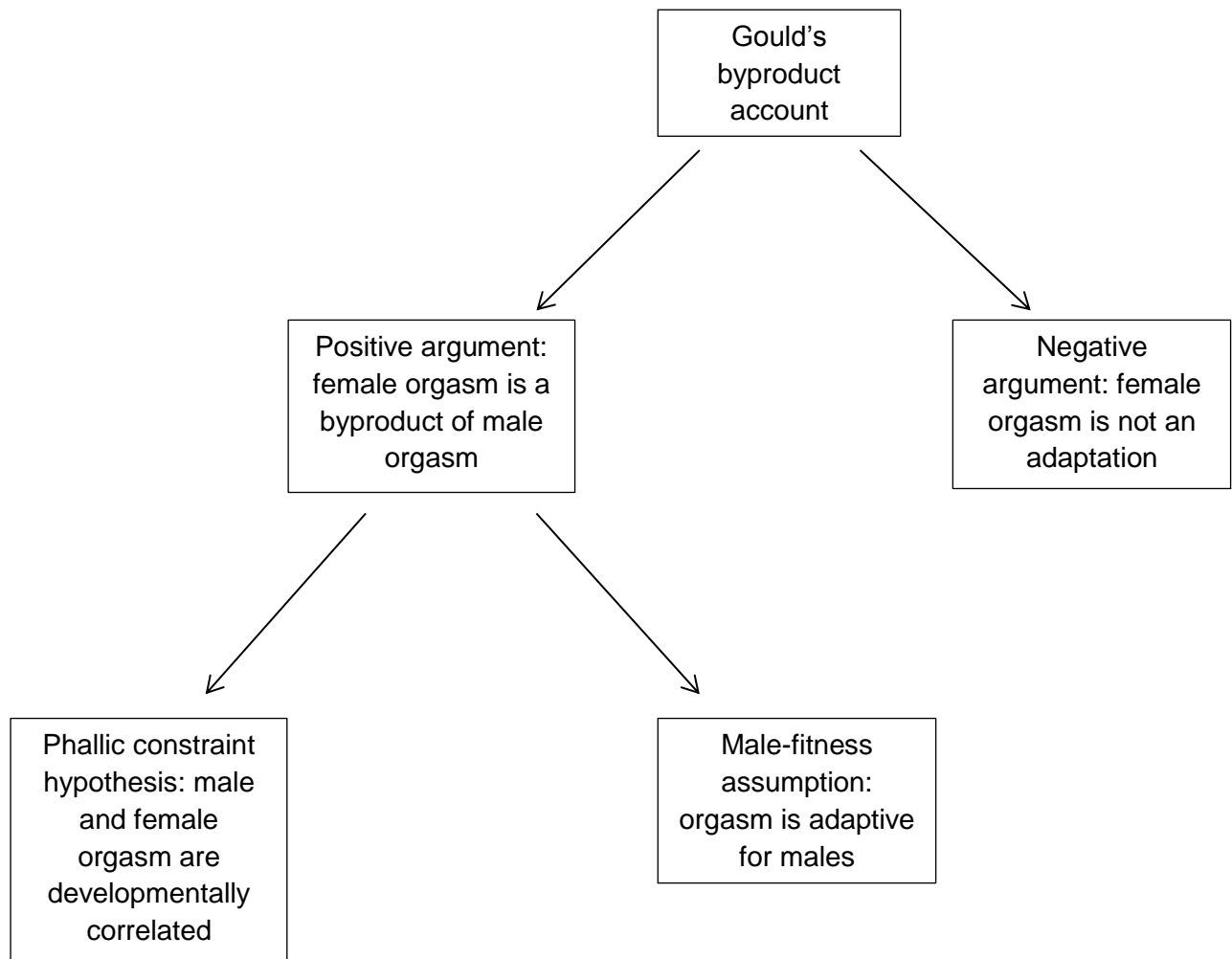
Throughout the literature, there is a tendency to treat the byproduct theory as a single, homogenous argument. However, it actually consists logically of two arguments (Lee 2013, p. 1021). One is a positive argument, regarding what female orgasm *is*. The other is a negative argument, regarding what female orgasm *is not*. Specifically, the negative argument is that female orgasm is not an adaptation. Although this argument has occupied the centre of attention in the debate over female orgasm, the present paper takes no position on this question. It is concerned with the positive argument only. Furthermore, it focuses on Stephen Jay Gould’s account because his contains a revealing link with the problem of developmental constraint.

Much has been made of Gould’s comparison of female orgasm with male nipples. However, it is more instructive to examine another example Gould uses to “help us to understand the general principle.”(1987, p. 16) It involves the classic ‘panda’s thumb’, an enlarged radial sesamoid with thumb-like function. The key detail is that “the corresponding bone of the foot, the tibial sesamoid, is also enlarged in the same manner (but not nearly so much), although this increase of the tibial sesamoid has no apparent function.” (p. 16) The

point is that the two sesamoids are homologues, and so their developmental fates are linked such that both will evolve in parallel manner if at least one of them is selected for an adaptive function. As Gould makes clear, this is a case of developmental constraint, wherein the evolutionary trajectory of a trait is constrained by its place within an integrated whole. For Gould, female orgasm is another such case. Developmentally linked with male orgasm, it will be expected to evolve in the same direction. Accordingly, the fact that male orgasm is clearly adaptive is sufficient to explain the presence of its female homologue. For Gould, this ultimately negates the need for any adaptive explanation of female orgasm.

Gould clearly established the central place of developmental constraint in his argument, particularly by essentially likening female orgasm to the panda's tibial sesamoid. He also went so far as to claim that the adaptive significance of the male homologue is obvious enough to negate the need for an adaptive explanation of the female one. For Gould, constraint is sufficient to explain it, and it is this 'explanation' that all concerned have focused on, accepting or rejecting it together with the constraint. But we need not go as far as Gould did to take constraint seriously. Gould's positive argument can be broken down into two core components. The first is the claim that the phallic homology constitutes a developmental constraint. The second is the assumption that male orgasm is adaptive, being so closely linked with fertility. For the present purpose this second component can be discarded, as our interest is only in what would be implied by the existence of a constraint. Thus we are no longer dealing with an explanation of female orgasm, because we are agnostic about any selective advantage on *either* homologue in the past or present; the bare existence of orgasm itself is taken as given. This is precisely the stance that this paper will take, with the hope of removing a major epistemic obstacle to understanding what the possibility of developmental constraint actually means, in itself, to this debate. It is the developmental constraint component of Gould's argument, explicitly excluding any claim

about the adaptive value of male (or female) orgasm, that I will henceforth call the ‘phallic constraint hypothesis’. This hypothesis is the core subject of my argument. The basic structure of Gould’s byproduct account and its relation to the phallic constraint hypothesis is summarised in figure 1.



**Fig. 1** The structure of Gould’s byproduct account

### **3. The Phallic Constraint Hypothesis**

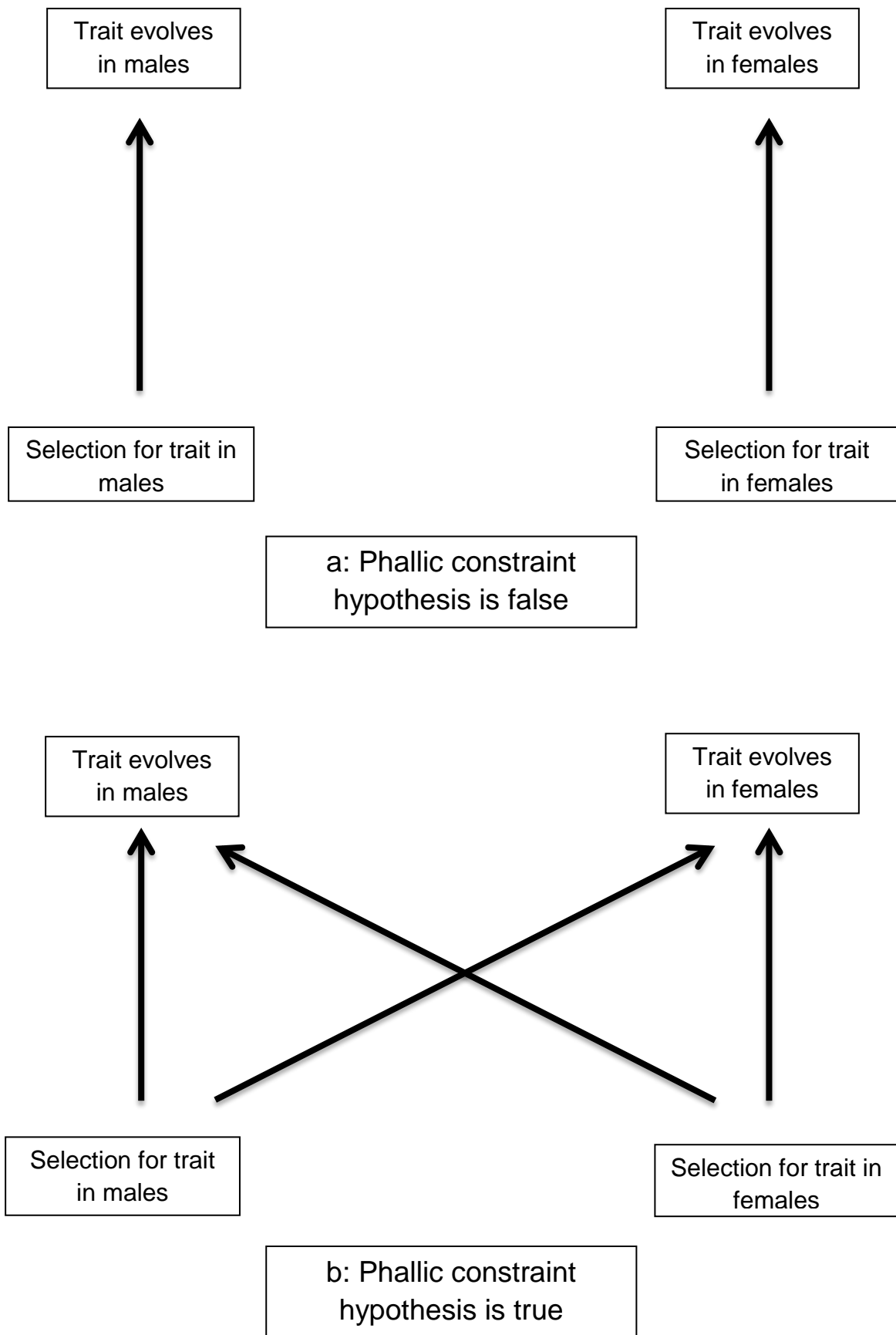
We can start by distinguishing between what is known and what the hypothesis requires. It is a fact that the site of orgasm in the female, the clitoris, is a developmental homologue of the male penis. Furthermore, this happens to include the pronounced innervation that is involved in orgasmic response. The two structures are homologous in the sense that their origins in the individual embryo are one and the same. The organ in an adult stemming from this precursor is called the phallus, whatever particular form it may take (penis or clitoris). This much is not controversial.

The phallic constraint hypothesis, however, goes further. It requires that the capacity to respond with orgasm to the right stimulation is more or less intrinsic to the phallus i.e. that the function emerges from the form. It further requires that this form (the orgasmically responsive phallus) is so entrenched in the developmental program that it cannot, at least easily, be rooted out in one sex while being maintained in the other. To put it another way, no single individual could either develop this system or not develop it depending on genotypic or phenotypic sex. The developmental program does not allow such radical sexual dimorphism, so that a significant correlation in the appearance of the same form (again including the function under consideration) between the two sexes is basically necessary. Selection cannot easily separate them.

The question is: what would this constraint do? Suppose that the phallic constraint hypothesis is false. The orgasmic function of the clitoris is independent from that of the penis and so the existence of female and male orgasm are theoretically consequences of selection for female and male orgasm respectively. Male orgasm exists because of selection on male orgasm. Female orgasm exists because of selection on female orgasm. What happens when we introduce the phallic constraint hypothesis into the equation? Now the function is tied

between the sexes and so it follows that the existence of either is a consequence of selection on both. Male orgasm exists because of any selection upon male *and/or* female orgasm. Likewise, female orgasm exists because of any selection upon orgasm in either sex. What was otherwise two separate pathways from selection to appearance, has become rather a pair of inputs into a single system with a two-fold outcome (Fig. 2).





**Fig. 2** The bearing of the phallic constraint hypothesis on the structure of selection

The selection dynamic depicted in the lower part of figure 2 is not without precedent. It has been used in population genetics since Haldane in 1962 as a potential cause of polymorphism. (In this context, care should be taken not to confuse *polymorphism*, here referring particularly to the non-fixation of genotypes in the population, with sexual *dimorphism*). Haldane argued that a stable equilibrium of two genotypes at a given locus in a population is possible under far more scenarios than was generally recognised. In particular, he argued that it might occur as a consequence if “the same gene substitution affects the fitness of the two sexes in a diploid in opposite directions.” (1962, p. 1108) This ‘opposite directions’ view is a very strong form of a more general idea: that selection on a given allele can operate differentially between the sexes because the allele confers different fitness values to each sex. Such ‘differential selection’ was further explored by Li, who focused on selection coefficients, for each sex, *against* the same genotype. Significantly, he pointed out that if this difference in selective advantage between the sexes is slight, “the average value of the two selection coefficients may be taken as the common selection coefficient for both sexes.” (1963, p. 493) Keeping in mind that it only takes a slight fitness advantage to potentially drive a trait to fixation, this statement appears to describe the phallic constraint hypothesis’ selection dynamics rather well.

More recently, differential selection has been implicated in the recessive genetic disease idiopathic haemochromatosis (IHC). IHC is characterised by enhanced iron absorption, which can lead to toxic iron overload, although this typically occurs in the post-reproductive years and is known to affect men far more frequently than women. However, enhanced iron absorption can also be advantageous, particularly for women because of iron loss through menstruation, lactation and pregnancy (which also explains their diminished chance of overload). For this reason, Rotter & Diamond regard IHC as another case of disease which, like sickle cell anaemia, is selected for the benefit of some individuals at the expense of

others. In this case, “men suffer and women benefit,” (1987, p. 289) hence differential selection. They further state that “[f]rom an unbiased evolutionary view, the deaths of some post-reproductive males are a small price to pay for protecting many women in the same population against anaemia.” (p. 289) This remark suggests that technically men do not actually suffer in terms of fitness. The disease itself is effectively invisible to selection, and exists because of its associated benefits for women.<sup>1</sup> Stated this way, Rotter & Diamond’s account of IHC bears a remarkable resemblance to the byproduct account of female orgasm.

In fact, if we abandon the focus on polymorphism in which the concept of differential selection has been used in this literature, what we find is a useful way of describing the logic of the byproduct account, namely in the language of population genetics. Suppose that orgasm is a direct phenotypic consequence of a single gene  $x$ . The key to understanding the consequences of this gene turns out to be that crucial distinction of creationist confusion: the randomness of mutation and the *non*-randomness of selection. If gene  $x$  is randomly introduced into a population, that means it does not distinguish between males and females (assuming the gene is not located on a sex chromosome). If the phenotype of gene  $x$  serves a reproductive advantage which is tied to male physiology, then the gene will be selected, not just non-randomly, but differentially. It will spread in the population as a consequence of a male-specific fitness benefit. That is, on average, mating pairs where the male possesses  $x$  will out-reproduce those where the male does not. Whether or not the female possesses  $x$  in any given mating is irrelevant. Because this bias in fitness benefit has no logical effect on the ratio of males to females among the offspring, there remains no bias in the presence of  $x$

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<sup>1</sup> Given the general discussion of costs and benefits, the ‘post-reproductive’ designation actually presents an inconsistency, at least in the absence of further elaboration. It also raises the question of what prevents the gene from reaching fixation in the population. This issue depends on genetic details beyond the span of the concise account given above. For a proper discussion, which makes the fitness costs of IHC explicit, see Livingstone (1992).

between the sexes. It is still distributed 50/50 between them, as was the case when it first appeared at random. The gene reaches fixation on the basis of strict differential selection.<sup>2</sup>

Although differential selection is associated with polymorphism, all that it necessarily amounts to is a constraint correlating features between the sexes. In its conventional genetic framework this constraint takes the most simple form imaginable: that the trait in each sex is caused by the same gene! This is the case with IHC, as well as the gene  $x$  analogy of orgasm given above. The phallic constraint hypothesis supposes a far more complex developmental equivalent: a trajectory of phenotypic expression too conservative for significant divergence between the sexes. Here, ‘significant’ would mean sufficiently divergent that the trait can be treated independently in either sex. The standard adaptationist view of female orgasm, by contrast, supposes the equivalent of a pair of genes, one for each sex, behind the same trait. In any case, the difference between the existence and non-existence of a constraint correlating male and female phenotype is the difference between the two radically different selection dynamics contrasted in figure 2.

#### **4. Developmental Biology**

To understand the full implications of the phallic constraint hypothesis, it is necessary to relate it to a more general controversy: should evolutionary biology be integrated with developmental biology? Should development continue to be treated as a black box within the traditional population genetics approach of the modern synthesis? Or should the contents of that black box be incorporated into evolutionary theory? This dichotomy can be expanded into three alternative positions:

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<sup>2</sup> This simplistic story was originally conceived as a way to explain the byproduct account to a layperson. In particular, it was a response to the false impression that orgasm is meant to *appear first* in the male. Explained with more precision (i.e. stating the conditions), and using just two generations, it proved successful with this particular individual. I recommend it as a very useful and helpful way to think about and describe the byproduct account, and of course the phallic constraint hypothesis. Furthermore, it shows how the arguments are not just about ‘development’.

- Position A: developmental detail is *always* relevant and as such no evolutionary account is complete without it.
- Position B: developmental detail is *at least sometimes* relevant and as such evolutionary accounts should include it whenever it appears necessary for avoiding unrealistic atomisation etc..
- Position C: developmental detail is *never* relevant. Evolution is strictly the province of population genetic details external to the developmental black box.

Which of these positions best fits Mayr's notion of adaptationism rightly practiced? The sheer fact that it is adaptationism seems to militate against position A. However, it does not appear to fit position C either, because that would seem to ignore developmental constraints altogether. Rather it is position B that seems to correctly follow from Mayr. This presents us with a problem. In a different context, namely that of the proximate/ultimate distinction, it is not position B but in fact position C that Mayr and others are advertising. Development concerns proximate explanations only. Getting it tangled up with ultimate explanations is considered "confusion". In this rhetoric, the constraining role of development seems to be completely forgotten. How might we explain this apparent inconsistency?

Amundson (1994) can help us understand by recognising that when developmentalists and adaptationists use the word 'constraint' they actually tend to mean different things. This is because the major gap between adaptationists and their detractors is not just opinion oriented, but disciplinary. Adaptationism is the standard practice of mainstream *evolutionary* biologists, namely those of the New Synthesis. Its most radical critics are generally *developmental* biologists, including those who wish to bring the two disciplines together, a perspective now articulated in evolutionary developmental biology (evo-devo). Amundson argues that one must turn to developmental sources of anti-adaptationist critique in order to

appreciate the extent of the divide. He thus tackles the developmental constraint line of argument in the context of a broader struggle over the ‘black-boxing’ of embryology by evolutionary theorists, and the developmentalist reaction.

In Amundson’s analysis, the root cause of the perspective differences lies in the different topics of interest between adaptationists and developmentalists. The former are concerned with the phenomenon of adaptation, while the latter are concerned with the phenomenon of form. Conversely, developmentalists have no particular interest in the bearing of form on adaptation, while adaptationists are *only* concerned with form inasmuch as it *does* bear on adaptation. It is precisely these divergent biases in professional interest that distinguish their respective concepts of constraint: to an adaptationist, any meaningful constraint is a ‘constraint on adaptation’; to a developmentalist, it means a ‘constraint on form’.

Developmental mechanisms can constrain the form of a structure by permitting only a finite number of possible/likely outcomes. But such a limitation need not have a constraining effect upon adaptation. This is because adaptation, in evolutionary language, is framed in terms of optimality. In this context, constraint means that optimality has been compromised. If any constraint on form (constraint<sub>F</sub>) has the effect of restricting the adaptive potential of a structure, then it also qualifies as a constraint on adaptation (constraint<sub>A</sub>). But if the organism in some way compensates for constraint<sub>F</sub> such that the same optimality can be achieved than would be without it, then it does not convert to a constraint<sub>A</sub>. That is, a constraint to a developmentalist does not entail a constraint to an adaptationist, because the concepts are distinct.

Two observations can be made of Amundson’s scheme. The standard definition of constraint comes to us from a classic paper by Maynard Smith and collaborators representing the consensus of a conference: “A developmental constraint is a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure,

character, composition, or dynamics of the developmental system.” (1985, p. 266, cited in Amundson 1994, p. 558) Amundson notes that this definition says nothing about adaptation, (1994, p. 569) which suggests that it can be identified with his constraint<sub>F</sub> rather than constraint<sub>A</sub>. The first observation, then, is that constraint<sub>F</sub> in a trivial sense describes what sorts of constraints actually exist, regardless of whether or not they are meaningful to an adaptationist. The second observation is that constraint<sub>A</sub> represents any constraint that *is* meaningful to an adaptationist. Although Amundson recognises the developmentalist perspective that “[t]he significance of developmental constraints cannot be reduced to the language of adaptive imperfection” (p. 575), he effectively conflates the significance of constraint for adaptationism with its capacity to reduce optimality. This shows us that even when adaptationists do take constraints into account, to state a truism, they have only a very particular idea of how it actually matters. If it does not place a limit on optimality, then it does not matter. The existence, by necessity, of innumerable constraints does not make every one relevant to a given hypothesis.

Amundson, then, presents us with a challenge. In order to establish the relevance of development for evolution, it must be shown that a constraint on form can affect evolution in ways other than simply limiting optimality in the same stroke as limiting form. It must have consequences for evolution which are effectively invisible to adaptationist modelling. Now the phallic constraint hypothesis is first and foremost a constraint on form. Furthermore, it determines the very structure of how selection on whom effects whom, consequently undermining the most basic premise of the adaptationists of female orgasm. Does it present a constraint on adaptation? In the case of existing adaptationist theories the answer is no, and for the same reason: it cannot limit parameters within a model while contradicting that model at the same time! The phallic constraint hypothesis suggests a case *par excellence* of

developmental biology interfering with evolution in a way that is irreducible to what adaptationist methods alone can intercept.

In this way, the phallic constraint hypothesis provides a confirming link to position B as the basis of good adaptationism. It does not advertise for a wholesale integration of development and evolutionary biology into a new consensus in favour of evo devo, but it does show that the argument that the details of development are straightforwardly irrelevant to evolution is simply unsustainable. Alcock's (1998) claim that the byproduct account is merely a 'proximate' explanation of female orgasm and so says nothing about its evolution is not just an 'extreme' view, as Lloyd (2005) portrays it, but it is demonstrably wrong, because that proximate mechanism is, according to the theory, a constraint that has everything to do with the trajectories of selection. In practice, the contents of the black box can always be *assumed* irrelevant, but never with certainty. Sometimes they demand serious consideration, and female orgasm presents a case in point.

## **5. Conclusion**

By effectively ignoring the very possible developmental connection between male and female orgasm (a constraint) and treating the two as mutually independent, the adaptationists of this debate have left themselves wide-open to the charge of atomisation, a cardinal sin according to the conservative standards of Mayr. The official right way to be adaptationist has not been lived up to, and a key complaint of Gould & Lewontin remains relevant.

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