

ENDS, NORMS, AND REPRESENTATIONS: WHY ASK
“WHY?” IN BIOLOGY

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Brandon Allen Conley

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Ends, Norms, and Representations: Why ask “Why?” in Biology?

Brandon Allen Conley

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In this dissertation I address three philosophical problems in the philosophy of biology united by the underlying, and interlocking, issues of the explanatory role of teleological, normative, and representational concepts in biology.

In the first chapter, I argue that extant accounts of functions have foundered on a problem I dub the Dysfunction Dilemma, and I offer a way to move forward. Functions are of philosophical interest because the concept plays an important explanatory role in biology, and other sciences, but is apparently teleological and normative—an item’s function is its end, purpose, or goal, and a dysfunctional item is one that fails to realize a particular norm, performance of its proper function. Extant accounts of function do not successfully capture both its explanatory import and its normative and teleological character, either painting dysfunction as conceptually incoherent or painting functions as epiphenomenal. I diagnose the source of the dilemma and offer an account of functional explanation which avoids it.

In the second chapter, I defend the idea that genes, like words or concepts, have intentionality or representational/semantic content. First, I argue that while the standard motivation for this idea is mechanistic analogies between molecular mechanisms and digital computation, Ernst Mayr, one of the architects of the modern synthesis in biology, has provided an alternative and more defensible justification for taking the idea seriously. Parallel to the standard case for representational and computational theories of cognition, Mayr’s justification rests on the need to invoke representations to explain end-directed processes. I then put Mayr’s argument to work answering three kinds of

objection to the idea that genes are representational: 1) Genetic representations are causally or explanatorily inert, 2) Genetic processes are too complex and context sensitive to be captured by representational concepts, and 3) Details of molecular biology undermine representational conceptions of genes.

In the final chapter, I develop a historical and philosophical interpretation of Ernst Mayr's distinction between proximate and ultimate causes and its relation to Niko Tinbergen's "four questions." Both frameworks have been influential in the biological study of behavior and are typically presented as a single framework, with Mayr's proximate-ultimate distinction corresponding to one of two axes dividing Tinbergen's four questions. I argue that this interpretation misrepresents Mayr's and Tinbergen's philosophical positions. I offer a positive account of both frameworks and their relation to one another, and I argue that contrary to many critics, Mayr's proximate-ultimate distinction, when properly interpreted, does not present a barrier to the project of integrating biological work on Tinbergen's four questions.

BIOGRAPHICAL SKETCH

Brandon Conley attended Appalachian State University, near his home town of Wilkesboro, NC, as a first-generation college student. There he received a Bachelor of Arts degree in both mathematics and philosophy, before pursuing his doctoral degree at Cornell University.

I would like to dedicate this dissertation to my parents, Allen and Betty Conley. When I once asked their feelings about my choice to pursue academia, and philosophy in particular, my mother responded “honestly, we don’t really understand what you do, but it seems to make you happy, so it’s fine with us.” It does make me happy, and so did that response.

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Introduction

1. Overview

In this dissertation, I explore the explanatory role of three interrelated phenomena in biology: teleology, normativity, and intentionality. The central thesis is that all three play an important explanatory role in biology, and the central task is to begin elucidating it. However, I do not take the approach of building a master argument over the course of the following chapters. Rather, each chapter is an independent argument focusing on one of the three in the context of a particular philosophical problem concerning biology. This approach allows for me to avoid attempting to treat one of the three phenomena of concern as more basic than the others, since I do not believe any of the three can nor need be reduced or fully explicated in terms of the others. But, neither do I think any of the trio can be satisfactorily treated without raising issues about the other two, and each is discussed to some degree in each chapter. The net result is that, while each chapter can largely stand alone, together they paint a coherent overall picture.

Focusing each chapter on a specific problem that arises independently of my own general concern about the explanatory role of teleological, normative, and intentional concepts also serves to make the arguments of the dissertation more grounded in concrete, specific problems than would be possible in an abstract discussion of these three phenomena in general. In the first chapter, I argue that extant philosophical accounts of the notion of function, which plays a central role in biological explanations, founders on a problem I dub the Dysfunction Dilemma. I develop a solution to the problem and develop a positive account of the explanatory role of the concept of dysfunction in biology and the sciences more generally. In the second chapter, I offer a defense of the idea that genes, like words and concepts, possess intentionality or semantic content. My case rests on the contention that rather than motivating representational and computational conceptions of genes on analogies between molecular mechanisms and digital computation, we should follow biologist Ernst

Mayr in invoking genetic intentionality to explain end-directed biological processes like development and behavior. I argue that Mayr's argument for genetic intentionality is parallel to the standard argument for representational and computational theories of mind in cognitive science, and then draw on this parallel to answer some extant critiques of genetic intentionality. Finally, the third chapter offers a historical and philosophical analysis of Mayr's influential distinction between proximate and ultimate causes, and its relationship to Niko Tinbergen's equally influential "four questions." Contrary to the standard reading of Mayr and Tinbergen, I argue that the two frameworks highlight distinct explanatory boundaries and that claims that Mayr's framework is a barrier to integrative work are unfounded.

In this introduction, I will summarize the three chapters individually in more depth and say a bit about their interrelations. The work here is intended to lay the groundwork for a broader philosophical project of defending a particular brand of philosophical naturalism, and of applying that framework to empirical and theoretical issues concerning the nature and origins of cognition, language, and prescriptive normativity, including morality. So, after summarizing the dissertation itself, I will briefly outline the broader philosophical motivations of this project. This broader outlook is not essential for grasping or appreciating any of the three chapters individually, but I believe that it brings into relief the picture of biological explanation that the three chapters together support, and its philosophical import.

2. Chapter 1: Dissolving the Dysfunction Dilemma

The first chapter addresses the role of normativity, and to a lesser extent teleology, in biological discourse through the concepts of dysfunction and proper functioning. Functional explanation, in not only biology but also the life, cognitive, medical, engineering, and social sciences more generally, has been a target of philosophical analysis at least since the late 1950's because of its apparently normative and teleological character.¹ The normative dimension is embodied in the idea

that an item that is properly functioning is one that does what it *ought* to do, while a dysfunctional item does not. The teleological character is captured by the idea that an item's function is its *purpose* or what it is *for*. The central puzzle is how to make sense of this normative and teleological character given that 1) biology seems to make ineliminable use of functional explanations in its explanatory practices, but 2) dominant conceptions of scientific explanation appear to leave no room for the normative and teleological to play any role, at least absent human purposes and norms. However, that functions appear to combine normative and teleological character with explanatory utility has made them an attractive tool for explicating other putatively explanatory but normative and/or teleological concepts. Most notably, functions occur in some prominent accounts of intentionality²—a link with the rest of the dissertation I note but do not explore in this chapter—and in some prominent accounts of the concept of disease.³ In *Dissolving the Dysfunction Dilemma*, I focus on the distinction between dysfunction and proper functioning.

The Dilemma is this:

- **Choice:** Either (A) Being capable of φ -ing is a necessary condition for possessing the function of φ -ing, or (B) Being capable of φ -ing is not a necessary condition for possessing the function of φ -ing.
- **Horn 1:** If A, then dysfunction attributions are incoherent, and much apparently good science emerges as conceptually confused.
- **Horn 2:** If B, then functions are causally inert (epiphenomenal), and much apparently good science emerges as explanatorily empty.
- **Dilemma:** Either way, our philosophical account of functions is at odds with uncontroversially successful scientific practices.

The two horns of the dilemma map onto the two major approaches to explicating functions, causal role accounts and etiological accounts. According to causal role accounts, an item's function

is its contribution to the workings of some larger system. For example, hearts have the function of pumping blood because the capacity to pump blood is their contribution to the capacity of the circulatory system as a whole to transport materials through the body. According to etiological accounts, an item's function is that which explains its existence through a process of design or natural selection. For example, hearts have the function of pumping blood because hearts have been favored by natural selection due to their ability to pump blood. Causal role accounts have been widely taken to render the concept of dysfunction incoherent because a dysfunctional item lacks the capacity to perform its function, but an item's contribution to a larger system cannot be a capacity it lacks. Etiological accounts, on the other hand, have been widely taken to make functions epiphenomenal because they divorce function possession from facts about an item's current causal powers, instead making it depend entirely on history. Both problems leave current accounts of functions unable to capture uncontroversially successful scientific practice, so we are left with a dilemma.

After arguing that extant views that might appear to avoid the dilemma do not, I offer a solution that begins with an argument that the first horn relies on an equivocation. The argument that causal role accounts renders dysfunction incoherent conflates different capacities because it ignores the role of what I call *triggering conditions* in individuating capacities. With this error in view, I develop a simple formal model of causal role functions that includes the notion of dysfunction and reveals that the concept allows us to express and reason about finer grained causal information than function attributions alone express. In short, an item has the function of φ -ing if its capacity or disposition to φ plays a particular causal role in a system, but whether it is dysfunctional or properly functioning depends on *under what circumstances* it manifests that capacity or disposition.

However, this argument is not simply a defense of causal role accounts over etiological accounts. I argue that insights from etiological accounts along with considerations from the

philosophy of science literature on natural kinds are necessary to explicate how the formal model I develop meets scientific practice. Only systems of certain kinds that arise through specific kinds of historical processes will tend to have the features that make functional explanation useful, and the operation of these processes, along with our explanatory goals, determine under which circumstances an item must perform to count as properly functioning. Avoiding the equivocation that leads to the first horn undermines the conflict between causal role and historical conceptions of function. By linking history and causal role, my account undermines the second horn as well. The Dysfunction Dilemma, therefore, is not so much solved as *dissolved*.

3. Chapter 2: Do Genes have Intentionality?

Biologists often apply representational concepts to genes. Genes are likened to blueprints, maps, codes, programs, recipes, or instructions for building an organism. These ways of talking seem to treat genes as though, like words or concepts, they have intentionality. That is, they presuppose that genes refer to or denote traits in the same way the word ‘dog’ and the concept DOG denotes dogs—John Maynard-Smith has explicitly made this claim.⁴ Philosophers have attempted to elucidate the theoretical role of this talk, but they have by and large taken a critical or deflationary stance. Though a few have attempted to offer positive accounts of the sense in which genes are representational,⁵ most have argued that the representational conceptions of genes are metaphorical, mistaken, or simply theoretically idle.⁶ I defend the idea that genes have intentionality by arguing that we should rethink the motivations for thinking genes represent traits.

The idea that genes are a kind of code or representation originates with the discovery of the mapping between nucleotide triplets and amino acids, a discovery that was aided by thinking of genes like Morse code. And, like the mapping of a language or code to its domain, this mapping is arbitrary, in the sense that other equally effective mappings were possible. The success of this approach encouraged the idea that genes operate by means mechanistically analogous to a digital

computer, with genes coding for a set of instructions for building an organism. However, I argue that biologist Ernst Mayr, who also made contributions to the history and philosophy of biology, offered an alternative motivation for thinking genes have intentionality, one which suggests answers to some of the primary criticisms of genetic intentionality.

Specifically, Mayr argues that a program offers the only known mechanism for genuinely goal-directed processes—that is, teleological processes. While natural selection explains how goal-directed systems can come into existence without an intelligent designer, programs explain how this goal-directedness is realized in the system selection builds. This is the same motivation for the foundational assumption of cognitive science that cognition is representational and, more specifically, computational. Both Mayr's argument and the usual case for representational theories of mind say that to explain end-directedness we must posit items with both causal and semantic properties. In slogan form, representations can generate end-directedness because semantics is mirrored by syntax which is in turn mirrored by causally relevant orthographic properties.

I do not defend this argument in the dissertation, but assuming that it is cogent, I argue that it makes genetic intentionality much more plausible and suggests means of answering common criticisms. I group common criticisms of genetic intentionality into three categories: 1) causal/explanatory inertness, 2) context sensitivity, and 3) implementational details.

The challenge of explanatory inertness arises in two forms. The first problem is that debates about the cogency of genetic intentionality have tended to proceed under the assumption that if any view of intentionality will be applicable to be genes, it will be teleosemantics, which defines semantic content in terms of a history of selection. The same problem of epiphenomenalism I discuss in Chapter 1 under the heading of etiological theories of functions arises for teleosemantics, because teleosemantics is an application of an etiological theory of functions to an account of intentionality. It is clear why biologists and philosophers of biology would gravitate to teleosemantics, but I argue

that the theoretical fate of genetic intentionality should not rest with that of teleosemantics. I argue that Jerry Fodor's asymmetric dependence theory provides one viable alternative, but I suggest that the most promising route would be a view that invokes the account of functions I defend in my first chapter. Here the issue of normativity arises, since the problem is providing an account of semantics that makes sense of the distinction between veridical and non-veridical representation. My own account preserves the normative dimension of functions without sacrificing their causal efficacy, so an account of intentionality that invokes this account might avoid making genetic representation causally inert while capturing the normative distinction between accurate representation and misrepresentation. However, I do not develop details of such an account here or hinge my argument on the correctness of my Chapter 1 account. The main point in this part of Chapter 2 is that teleosemantics is not the only option, and that epiphenomenalism is a problem with teleosemantics not with genetic intentionality.

The second form in which the problem of causal/explanatory inertness arises is that some have alleged that talk of genetic programs or representations engenders a false sense of explanatory completeness, precluding researchers from addressing important questions about mechanisms.⁷ For example, saying that a genetic program controls limb development gives the impression that limb development has been explained but in fact leaves much of the process mysterious. In response, I argue that biologists employing representational concepts should keep in view important distinctions already recognized in cognitive science. David Marr's distinction between computational, algorithmic, and implementational levels of explanation and the division in linguistics between orthography/phonology, syntax, semantics, and pragmatics, would both prevent these sorts of errors. Though, I have little doubt the phenomenon these critics cite is real, it is a mistake arising from misconceptions about the nature of explanations invoking representations rather than a problem with the idea that genes are representational.

Both of these responses to the problem of causal inertness arise naturally from a conception of genetic representation motivated by the need to explain end-directedness. This is because 1) this theoretical motivation highlights parallels with cognitive science, making the distinctions and theoretical options in cognitive science salient, and 2) moving away from motivating genetic intentionality through mechanistic analogies with digital computers removes the background presumption that representational conceptions of genes come pre-packaged with an understanding of the mechanisms implementing the representational/computational system. Instead, representations are posited to explain specific end-directed processes, leaving as a questions for further research the details of the representational/computational processes and their implementation.

The second major objection to genetic intentionality is that representational conceptions of genes fail to capture the complexity and context sensitivity of the causal connection between genes and traits. Again, I suggest that parallels with cognitive science suggest a response. If we look at how the most well studied naturally occurring representational systems, natural languages, actually work, there is no grounds for the claim that representational conceptions are too simple or context insensitive to capture the causal role of genes. My point is not simply that language can be context sensitive but that an examination of what linguists and philosophers of language have learned about natural language reveals it to be uncontroversially wildly context sensitive. And, a realistic view of how a given term relates to its referent reveals it to be wildly complex.

While a conception of genetic representation arising from simple analogies with Morse Code and digital computation may encourage inferences that covertly rely on simplistic assumptions about the relationship between genes and traits, a conception theoretically grounded in cognitive science does not. Rather than abandoning representational conceptions of genes, we should make sure biologists who employ them have a realistic view of how representational systems like natural

language actually work. I suggest that those critics concerned to de-emphasize the role of genes in development should adopt a broader conception of representation exemplified by movements in cognitive science toward embodied cognition, which emphasizes the environmental and embodied locatedness of cognitive processes.

Finally, I argue that more generally we should be wary of critiques that move from details of molecular biology to claims about the cogency of representational conceptions of genes. Again, I invoke Marr's distinctions between implementational, algorithmic, and computational levels, this time to argue that we should expect molecular details to be largely irrelevant to claims about genes representing traits. Additionally, given that the motivation for thinking genes have intentionality is to explain end-directedness, we should expect that, as with other cases of this explanatory strategy in cognitive science and the theory of computation, there will be multiple representational levels. Just as the semantics of a machine code in a digital computer are different from the semantics of high level programming languages implemented in that machine code, we should expect the semantics of low level genetic representations closely tied to mechanistic details to differ from the semantics of higher level representations implemented by the genome more holistically. I end this section by noting that it is also possible for theoretically useful high level representational descriptions to be abstracted from or only implicitly implemented in lower level representations. These three considerations all tell against the relevance of molecular details to claims about genes representing traits, but they also suggest that the relationship between genes in traits is holistic, a point that coheres well with what most critics of intentionality are really out to establish.

4. Chapter 3: Disentangling and Integrating Mayr and Tinbergen

In the final chapter I offer a philosophical and historical elucidation of the influential frameworks developed by Ernst Mayr and Niko Tinbergen for dividing the explanatory labor in biology. Ernst Mayr was an evolutionary biologist who made significant contributions to the history

and philosophy of biology in the later part of his career. Tinbergen was one of the founders of the field of ethology and developed much of the conceptual framework that has organized research in ethology, and its descendant fields like behavioral ecology and sociobiology.

Tinbergen divided biological research into a search for answers to four kinds of questions, evolutionary, survival value, mechanistic, and developmental.⁸ Mayr divided biological research into a search for ultimate causes that answer “why?” questions and proximate causes that answer “how?” questions.⁹ Typically, biologists take these two frameworks to be unified, with Mayr’s proximate-ultimate distinction marking one of two axes dividing Tinbergen’s four questions. Evolutionary and survival value questions are taken to correspond to Mayr’s “why?” questions, while mechanistic and developmental questions correspond to Mayr’s “how?” questions. My central claim in Chapter 3 is that this picture is misleading. Mayr’s distinction does not map cleanly onto Tinbergen’s. Mayr would only class as ultimate a subset of the causes that are invoked to answer evolutionary and survival value questions, and Mayr recognizes a third category beyond proximate and ultimate which he calls “the role of chance.”

In addition to the intrinsic philosophical and historical value of elucidating Mayr’s and Tinbergen’s frameworks and their relationship, my account is relevant to current methodological debates about integrative research. Mayr’s philosophical goal was to defend the autonomy of evolutionary biology in the face of reductionist challenges, and this creates a tension with Tinbergen’s philosophical goal of integrating different disciplines and sub-fields concerned with animal behavior. This tension has led several commentators to advocate rejecting Mayr’s distinction on the grounds that it is a barrier to integrative research.¹⁰ I argue that this tension vanishes when the two frameworks are properly interpreted.

In the context of this dissertation, a key motivation for tackling this historical interpretive task is that Mayr’s proximate-ultimate distinction forms part of his, I think very useful, account of

the role of teleology in biology. Additionally, I argue that the best interpretation of Tinbergen's and Mayr's conception of integration is that they both adopt a causal role approach to functions, of the kind I address in Chapter 1. And, the conception of genetic intentionality I defend in chapter 2 plays a key role in Mayr's characterization of the proximate-ultimate distinction through his use of the concept of a genetic program. The details of my other chapters plays no explicit role in my elucidation of Mayr's and Tinbergen's views, but these connections highlight the interdependence of the role of normative, teleological, and intentional concepts in biology.

I will not attempt to summarize my entire account of Mayr's and Tinbergen's views, because there are many moving parts. But, the key points are these: 1) Tinbergen's four questions represent different perspectives we can take on a single causal system, and he advocates integration through a process of functional analysis whereby the explanandum of one sub-discipline forms part of the explanans in another. 2) For Mayr, ultimate causes are only those cited as selective advantages in a narrative explanation at a population level. This may seem to conflate multiple distinctions, but Mayr is not conflating them; rather, he sees a particular *combination* of properties of explanations in evolutionary biology as essential to his anti-reductionist case. 3) For Mayr, it is ultimately the "teleological" nature of explanations in evolutionary biology that sets them apart, but I use scare quotes here because Mayr believes the term 'teleological' is misleading and conflates different phenomena. One sense is explicated by his notion of programs and the other by the particular narrative form of evolutionary explanations citing natural selection. The proximate-ultimate distinction marks this division. 4) But, Mayr recognizes Tinbergen's insights, and he recognizes that non-ultimate causes also play a role in evolutionary explanations. His case against reductionism is compatible with Tinbergen's conception of integration. 5) Mayr's notion of "chance" specifically denotes non-directional causes—or in his view constraints rather than causes—of evolutionary

change. Non-ultimate causes cited in evolutionary explanations either form part of an analysis of selection itself, or an analysis of the role of chance.

I remain neutral about the success of and need for Mayr's case against reductionism. I suspect there is something right about it but that reductionism of the form that worried Mayr can be undermined without his argument. Nevertheless, I have undertaken this historical project in part because I think Mayr has got a lot of things right, especially his picture of the relationship between representation and teleology, which paints a very different picture from the one suggested by teleosemantics. However, I focus more on elucidating than defending Mayr's views in this dissertation.

5. The Big Picture: Naturalism and Non-Reductionism

In this final section, I place my work in the context of the very big picture. At the broadest scale, my project is to develop and defend philosophical naturalism. In slogan form, this is the view that science and philosophy are continuous and that in some important sense, the sciences paint a complete picture of the world. But slogans do not hold up to philosophical scrutiny long, and most philosophers, even self-proclaimed naturalists, tend to characterize naturalism less as a thesis to be defended than a general philosophical style or inclination.¹¹ I do not agree. I believe but will not argue here that a careful look at the history and practice of naturalistic philosophy reveals patterns of methodological, ontological, and epistemological commitments that reveal a unified worldview, a complex of interlocking and reinforcing theoretical commitments that can be distilled down into a very basic insight. Naturalism is a kind of monism. Now, let me explain.

In short, humankind has gotten better and better at gaining knowledge, and around the period we call the scientific revolution, this pattern reached an inflection point, and we got very good very fast. One side effect is that we started learning a lot of things that clashed with our ordinary conception of ourselves. It just was not clear how to fit human purpose, language, thought,

or morality into the picture physics was beginning to paint, especially given the religious concepts that had largely formed our conception of these categories. The early modern period, I believe, can be largely characterized by the struggle to reconcile our self-image with the scientific one. And, in essence, the early moderns found two solutions. 1) We could fit our beloved categories into the scientific picture, somehow, perhaps modified, or we could draw a line segregating our self-image from the reach of science. On my view, naturalism is characterized by taking route 1. Route 2 is Kantianism—and, in my view, whether they recognize it or not, most philosophers are, at heart, Kantians. For example, (again I assert here but will not argue) various forms of pragmatism that claim to be naturalistic are really, on closer examination, Kantian.

Naturalists deny the kind of division between the empirical realm and the realm of the various things we care about like morality, meaning, and the seat of human thought that Kantians endorse. This leaves naturalists with the challenge of saying how those categories fit into the image of the world science paints for us. By and large, philosophers have only recognized one option, reduction.

I also assert, but will not argue here, that the problem cases for naturalism all boil down to the problem of making sense of the three phenomena targeted in this dissertation, normativity, teleology, and intentionality. Thus, naturalistically inclined philosophers have, for the most part, been preoccupied in one form or another with providing naturalistic reductions—we even have a term for it, ‘naturalizing’—these three categories. However, I believe we have every reason to suspect that the task is impossible and unnecessary.

Naturalizing some category or concept is typically taken to consist in providing a naturalistic definition. For example, naturalizing intentionality is supposed to take the form of necessary and sufficient conditions for something to be intentional, stated without recourse to any intentional or other naturalistically problematic category. However, if naturalists are right that teleology,

normativity, and intentionality are natural phenomena, then we have no reason to think they will be any more amenable to definitions of this reductive sort than any other natural phenomenon. That we find these concepts suspect does not induce the universe to make them explicable in other terms. Reduction can come in many forms, but there is broad agreement among philosophers that while it is pretty clear that everything is constituted out of physical stuff, the reduction of non-basic terms, concepts, theories, laws, and so on to the categories of more basic sciences—meanings sciences that study more basic stuff, in the sense that other stuff is composed out of it—is usually impossible. Those philosophers who disagree do not think these reductions will be forthcoming in practice or that they are necessary for vindicating the usefulness of the target categories. It is thus a non-starter to rest the case for naturalism on providing just these kinds of reductive accounts of the categories and concepts we find most vexing. That a concept appears naturalistically problematic indicates that its relation to other stuff in our world is even less clear than other things we already admit cannot be defined reductively.

This leaves us with the puzzle of how to naturalistically vindicate a problematic concept or phenomenon. The answer, in my view is that we vindicate these concepts in the same way we justify any concept from a scientific perspective. The much over-simplified process is this: 1) We show that the concept does useful explanatory work, indicating that it is not simply a fiction to be eliminated. 2) we show how in a few specific cases we can offer detailed stories about how the phenomenon is constituted out of the basic ingredients we already recognize and infer that similar stories can be given in other cases. But, crucially, we do not attempt to provide a general definition or reduction. The steps need not occur in this order and are not entirely separate.

The strategy can be seen in the history of biology with respect to the phenomenon of life. We no longer view life as naturalistically problematic, but at one time it was not easy to make it cohere with the image of the world arising from physics. We did not get past this problem by

providing a reductive definition of life in terms that make no reference to life. Rather, we characterized the useful explanatory work that justifies recognizing a distinction between life and non-life, for example localized and stable regions of high entropy and complexity. And, we slowly formed a picture of how specific bits of life are put together out of other ingredients, recognizing on the way many borderline cases. We cannot say exactly how most cells are put together or even which exact things count as cells, but we know how several specific kinds of cells are put together, and we rightly assume other cases will be similar and non-mysterious rather than vainly striving to produce a universal recipe or definition. In the process we have abandoned the search for a bright line separating life and non-life yet recognized enough of a distinctive explanatory role to justify recognizing separate categories anyway.

I conceive of this dissertation as an attempt to contribute to step 1 for teleology, normativity, and intentionality. My goal is to show that teleological, normative, and intentional concepts do valuable explanatory work in biology, indicating that they are part of the image of the world as painted by science. I begin with biology because it is the most basic science in which these phenomena seem to play an important role in explanation and the science in which their application is most problematic because, in most cases, the phenomena of interest to biologists are independent of human purposes, norms, and meanings. It is likely that teleological, normative, and intentional concepts in other fields can be illuminated by their role in biology, because the cognitive, social, and even engineering science (and the humanities, too), are concerned with phenomena that occur in the context of living organisms.

This dissertation also, more indirectly, contributes step 2 by showing how the three target phenomena interlock with one another and fit into the larger scientific enterprise. My account of functions vindicates a kind of normativity in science, but it does not provide a reductive account of the kind of prescriptive normativity at issue in ethics and politics. I suspect that kind of normativity

is partly explained by our motivations and attitudes, which embody a kind of intentionality. Intentionality, in turn, as I argue in chapter 2, is likely in part to be explicated with reference to my theory of functions and the brand of normativity it supports. My account of functions in turn relies on a kind of teleology, namely the ability of processes like selection and design to fit means to ends. This is not full-fledged purposiveness, which also likely requires a form of conceptual cognition, and thus intentionality. No one of the phenomena can be defined in a single step in terms of the others, and each arises in biology in a form that is recognizably part of but only part of our conception of them in the context of human language, purposes, and norms. This is as it should be on my conception of “naturalization.” The goal is to blur the boundaries between these categories and the naturalistically unproblematic ones. As with the concept of life, the ultimate goal is to remove any hope for a bright line separating normativity, teleology, and intentionality from the rest of the world, all the while highlighting their particular explanatory role in virtue of which they earn a place in a naturalistic ontology.

I will not attempt to outline here my ideas about where to go from here in any detail, but the rough path is this. I suspect many non-naturalist philosophers will object that the kinds of normativity, teleology, and intentionality I have shown to play a role in biology are not enough to capture the human categories like morality, thought, and language that naturalists need to account for. In a sense, I agree. But, the goal is not to provide the tools for a direct reductive definition. It is to show how versions of the phenomena we care about enter the scientific image, and provide ingredients for showing how to build up to the categories we care about. The next step, I believe, is to show how the kind of normativity I defend in chapter 1 can help explicate the notion of representation I defend in Chapter 2, and how this gets us from the kind of teleology Mayr sees in adapted systems to the kind explained by the operation of program. With such an account in hand, we are well on our way to demystifying both human cognition, including motivations and desires,

and illuminating our especially social nature. These two ingredients, combined with a recognition of the role of means-ends reasoning in evolutionary biology independent of any invocation of cognition, I suspect opens the door to a thoroughly realist naturalistic treatment of morality. But, as with my strategy in the dissertation, I believe these steps will be best accomplished through engagement with specific, often empirical, problems. So, my long term aims include applying the work in this dissertation to specific issues in philosophy of mind, language, and science, to ethics, and to the evolution of social behavior.

But first, I have promised a dissertation in which I offer an account of dysfunction, defend genetic intentionality, and offer a novel interpretation of Ernst Mayr's and Niko Tinbergen's explanatory frameworks. The success of none of these three specific projects hinges on the details of my broader naturalistic aims or methodological inclinations. Nonetheless, it is my hope that this foray into the very big picture highlights the unity underlying the dissertation and an idea of where I hope to take the work I begin here after this dissertation is printed and shelved.

Notes

¹ Early papers included, Morton Beckner, *The Biological Way of Thought* (New York: Columbia University Press, 1957); Carl Hempel, "The Logic of Functional Analysis," *Symposium on Sociological Theory* (New York: Harper & Row, 1959), reprinted in *Aspects of Scientific Explanation* (New York: The Free Press, 1965); and Ernest Nagle, *The Structure of Science* (New York: Harcourt, 1961); but terms of later debate were largely set by, Larry Wright, "Functions," *The Philosophical Review*, 82, 2 (April 1973): 139-168; and Robert Cummins, "Functional Analysis," *The Journal of Philosophy*, 72, 20 (November 1975): 741-765.

² Ruth G. Millikan, *Language, Thought, and Other Biological Categories: New Foundations for Realism* (Cambridge MA: MIT Press, 1984); "Biosemantics," *The Journal of Philosophy*, 86, 6 (June 1989): 281-297; Fred Dretske, *Explaining Behavior: Reasons in a World of Causes* (Cambridge MA: MIT Press, 1988); Karen Neander, "Misrepresenting and Malfunctioning," *Philosophical Studies: An International Journal for Philosophy in the Analytic Tradition*, 79, 2 (August 1995): 109-141.

³ Christopher Boorse, "Health as a Theoretical Concept," *Philosophy of Science*, 44, 2 (December 1977): 542-573; Jerome C. Wakefield, "The Concept of Mental Disorder," *American Psychologist*, 47, 3 (March 1992): 373-388.

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- ⁴ John Maynard-Smith, “The Concept of Information in Biology,” *Philosophy of Science*, 67, 2 (June 2000): 177-194.
- ⁵ Kim Sterelny, Kelly C. Smith, and Michael Dickison, “The Extended Replicator,” *Biology and Philosophy*, 11, 3 (July 1996): 377-403; Nicholas Shea, “Representation in the Genome and in Other Inheritance Systems,” *Biology and Philosophy*, 22, 3 (June 2007): 313-331; Nicholas Shea, “Inherited Representations are Read in Development,” *British Journal for the Philosophy of Science*, 64, 1 (March 2013): 1-31.
- ⁶ Susan Oyama, *The Ontogeny of Information* (Cambridge: Cambridge University Press, 1985); Sahotra Sarkar, “Decoding “Coding”—Information and DNA,” *Bioscience* 46, 11 (December 1996): 857-864; Peter Godfrey-Smith, “Genes and Codes: Lessons from the Philosophy of Mind?,” in Valerie Hardcastle (ed.), *Biology Meets Psychology: Constraints, Conjectures, Connections* (Cambridge MA, MIT Press, 1999); Peter Godfrey-Smith, “On the Theoretical Role of “Genetic Coding”,” *Philosophy of Science*, 67, 1 (March 2000): 26-44; Philip Kitcher, “Battling the Undead: How (and How Not) to Resist Genetic Determinism,” in R. Singh et al (eds.) *Thinking About Evolution: Historical, Philosophical, and Political Perspectives (Festschrift for Richard Lewontin)* (Cambridge, Cambridge University Press, 2001); Paul E. Griffiths, “The Fearless Vampire Conservator: Philip Kitcher, Genetic Determinism, and the Informational Gene,” in E. M. Neumann-Held and C. Rehmann-Sutter (eds.) *Genes in Development: Re-reading the Molecular Paradigm* (Durham NC: Duke University Press, 2006); Arnon Levy, “Information in Biology: A Fictionalist Account,” *Noûs*, 45, 4 (December 2011): 640-657; Paul E. Griffiths and Karola Stotz, *Genetics and Philosophy: An Introduction* (Cambridge: Cambridge University Press, 2013).
- ⁷ Robert Lickliter and Thomas D. Berry, “The Phylogeny Fallacy: Developmental Psychology’s Misapplication of Evolutionary Theory,” *Developmental Review*, 10, 4, (December 1990): 348-364.
- ⁸ Niko Tinbergen, “On the Aims and Methods of Ethology,” *Zeitschrift für Tierpsychologie*, 20, 4 (1963): 410-433.
- ⁹ Ernst Mayr, “Cause and Effect in Biology,” *Science*, 134, 3489, (November 1961): 1501-1506.
- ¹⁰ See especially Mary Jane West-Eberhard, *Developmental Plasticity and Evolution* (Oxford: Oxford University Press, 2003); Kevin Laland et al, “Cause and Effect in Biology Revisited: Is Mayr’s Proximate-Ultimate Dichotomy Still Useful?,” *Science*, 334, 1512, (December 2011): 1512-1516; and Kevin Laland et al, “More on How and Why: Cause and Effect in Biology Revisited,” *Biology and Philosophy*, 28, 5 (September 2013): 719-745.
- ¹¹ See for example David Papineau, “Naturalism,” *The Stanford Encyclopedia of Philosophy (Winter 2016 Edition)*, Edward N. Zalta (ed.), URL = <https://plato.stanford.edu/archives/win2016/entries/naturalism/>; and Penelope Maddy, *Second Philosophy: A Naturalistic Method* (Oxford: Oxford University Press, 2007).

Chapter 1: Dissolving the Dysfunction Dilemma

1. Introduction

Function attributions play an important explanatory role in the life, cognitive, medical, social, and engineering sciences, and in the humanities and everyday discourse. They also appear to express that an item has a particular goal or purpose, and is subject to a particular norm, realizing its goal or purpose—an item that cannot is dysfunctional. Because dominant conceptions of scientific explanation allow no role for the normative or teleological, functions have become a target for philosophical explication and an attractive tool for explicating other putatively normative but explanatory concepts—most notably disease¹ and representation.² My aim is to argue that philosophical theories of functions have foundered on a problem I dub the Dysfunction Dilemma, and to offer a way forward.

Dysfunction Dilemma:

- **Choice:** Either (*A*) Being capable of φ -ing is a necessary condition for possessing the function of φ -ing, or (*B*) Being capable of φ -ing is not a necessary condition for possessing the function of φ -ing.
- **Horn 1:** If *A*, then dysfunction attributions are incoherent, and much apparently good science emerges as conceptually confused.
- **Horn 2:** If *B*, then functions are causally inert (epiphenomenal), and much apparently good science emerges as explanatorily empty.
- **Dilemma:** Either way, our philosophical account of functions is at odds with uncontroversially successful scientific practices.

The two major approaches to functions embrace opposite horns of the dilemma: Causal role theories opt for Horn 1 while etiological theories embrace Horn 2. After outlining both approaches

concurrently with the dilemma itself and arguing that three initially promising positions do not avoid the dilemma, I argue that the first horn arises from an equivocation. Avoiding the equivocation allows for an independently plausible account on which dysfunction attributions are not only coherent in a causal role framework but contribute to causal explanation. I develop the beginnings of such an account through a simplified model and then connect that model to practice by invoking considerations about natural kinds that vindicate insights from the etiological approach. The account unifies the theory of functions and dissolves the Dysfunction Dilemma.

2. Causal Role Functions

The canonical formulation of the causal role approach to functions is Robert Cummins's account of *functional analysis*.³ Cummins argues that an item's function is its causal contribution to the workings of some system. We can explain a disposition or capacity of a system of by decomposing it into simpler dispositions or capacities (sub-capacities), organized in a particular way. This decomposition is a functional analysis, and the sub-capacities are functions of the items that possess them. Cummins defines what it is to possess a function formally as follows:

x functions as a φ in [a system] S (or: the function of x in S is to φ) relative to an analytical account A of S 's capacity to ψ just in case x is capable of φ -ing in S , and A appropriately and adequately accounts for S 's capacity to ψ by, in part, appealing to the capacity of x to φ in S .

For example, the circulatory system has the capacity to transport materials like oxygen, waste, and hormones to different parts of the body. We can decompose this capacity into several sub-capacities including pumping, directing flow, diffusing materials, and so on. The heart's capacity to pump blood contributes to the system's capacity to transport material. So, the function of the heart (x) in the circulatory system (S) is to pump blood (φ) because the heart is capable of pumping blood (φ -ing), and the standard physiological account (A) of how circulatory systems work

adequately and appropriately accounts for the circulatory system's capacity to transport material (ψ), in part, by appealing to the heart's (x 's) capacity to pump blood (φ). I will address what makes an analytical account "appropriate and adequate" in a later section.

The first horn of the Dysfunction Dilemma is that causal role accounts appear to render the concept of dysfunction incoherent. For an item to be dysfunctional is for it to be unable to perform its function. The following argument is ubiquitous in the literature on functions, made by critics and defenders alike of causal role accounts, including Cummins.⁴ The conclusion is so widely accepted, and taken to be so obvious, that many simply assert it without bothering to rehash the argument.⁵

Premise 1: Assuming Cummins's definition, if something possesses the function of φ -ing, then it is capable of φ -ing.

Premise 2: An item is dysfunctional, with respect to the function of φ -ing, if and only if it has the function of φ -ing but is not capable of φ -ing.

Conclusion: Assuming Cummins's definition, an item is dysfunctional with respect to the function of φ -ing if and only if it is both capable of φ -ing and not capable of φ -ing

Cummins's definition of function implies that a dysfunctional item both is and is not capable of φ -ing, which is absurd, so dysfunction attributions are incoherent given a causal role conception of functions. I will argue in Section 5 that this argument fails because it relies on an equivocation, but the argument is taken to be obviously sound in the literature on functions, so to set up the Dysfunction Dilemma, let us accept it for now. Philosophers divide over whether this argument shows the causal role approach to be mistaken or dysfunction attributions to be incoherent.

Those who embrace the incoherence of dysfunction attributions do not claim that dysfunction attributions are meaningless, only that they are conceptually confused because they attribute functions to things that do not really have them. On this view, strictly speaking, something

that is not capable of φ -ing does not have the function of φ -ing. But, this does not entail that there is no difference between the things we confusedly call dysfunctional versus the things would not be tempted to say have the relevant function. According to Boorse, we call an item dysfunctional if it does not perform the statistically normal function for items of its kind.⁶ Dysfunction attributions are thus a loose way of expressing statistical claims. Paul Davies argues that we call an item dysfunctional when we expect or wish it to perform a certain function, so they reveal more about us than about the item characterized as dysfunctional.⁷

The only argument for this deflationary picture of dysfunction is that our best theories of function seem to force us into it. But, we should be wary of arguments from failures of those theories, especially since the only independent motivation for the view is a prior suspicion that normative concepts cannot possibly contribute to scientific explanation. Dysfunction attributions are routine, and apparently explanatory, in what looks like good scientific practice, so there is reason to think this suspicion is misguided.

When doctors or engineers call an item dysfunctional, it appears to play as much a role in their reasoning and communication as any function attribution, and there is no obvious reason to take them to be simply engaging in loose talk. There appears to be nothing strange about citing dysfunction, or closely related concepts, in causal explanations: The patient experiences fatigue when climbing stairs because she has a failing (i.e. dysfunctional) heart. The car did not start because the ignition malfunctioned. Cancer can be caused by a dysfunction in the gene copying machinery of the cell. Biologists define animal signals as behaviors with the function of carrying information,⁸ and the failure of some signals to perform their information carrying function is central to work in animal communication because the central question is how signals can evolve to be reliable. The most straightforward description of knockout experiments in neuroscience and genetics is that they rely on making causal inferences about a given gene or brain region by experimentally probing the effects

of rendering it dysfunctional. If a dysfunction has effects, then it must be causally relevant and therefore more than loose talk or expressions of our attitudes.

There are also functions which arguably presuppose a coherent notion of dysfunction. A backup system's function is to engage when the primary system fails to perform its function. Attributions of functions of error detection, repair, or redundancy all presuppose that one item's function can be to deal with dysfunction elsewhere in the system.

We may be able to rationally reconstruct or eliminate apparently explanatory dysfunction attributions, but the only argument that we can or should is that we have failed to develop a philosophy of functions that does not require it. But, dysfunction plays a bigger role in science than deflationists have recognized, and rational reconstruction has a poor track record. We should not let suspicion of normative concepts entice us too easily into painting apparently good science as conceptually confused, pending philosophical reinterpretation.

3. Etiological Functions

Etiological approaches to functions generalize the idea that an artifact's function is what it was designed to do to cases where there was no intentional design, by construing function attributions as an explanation for why an item exists. When we say that a spark plug has the function of igniting gasoline, we have a general idea of how the spark plug came to be—it was designed by people—and the function attribution fills in the reason or end that motivated the designer. Hearts have no designer, but we similarly fill into a general background theory the missing “end” that explains the heart's existence. The most popular version of this view says that the relevant background is a history of natural selection. Hearts have the function of pumping blood because pumping blood is what they were selected, rather than created, for.⁹ Since an individual item can fail to be capable of φ -ing but still be the kind of thing that was selected for doing so, or be the kind of thing that was designed for doing so, etiological accounts avoid the problem with dysfunction.

However, it is important to keep distinct the question of what relation an item must have to φ -ing to possess the function of φ -ing from the question of what relation an item must have to φ -ing to be dysfunctional with respect to that function. A deflationist about dysfunction might concede that we call an item dysfunctional if it does not perform the function of φ -ing that it was selected for but say that, strictly speaking, such an item does not possess the function of φ -ing because that would require that it be capable of φ -ing. It is not the invocation of history per se that allows etiological views to avoid rendering dysfunction incoherent, but the denial that being capable of φ -ing is a necessary condition for possessing the function of φ -ing.

Non-etiological views could use the same strategy. Say an item possesses the *Cummins-function* of φ -ing if it satisfies Cummins's definition of possessing the function of φ -ing. We could say an item has the function of φ -ing just in case it is statistically normal for items of that kind to possess the Cummins-function of φ -ing, or that an item has the function of φ -ing just in case we expect or desire that it have the Cummins-function of φ -ing. Neither view requires that an item be capable of φ -ing to have the function of φ -ing, so both make dysfunction attributions coherent.

However, by divorcing function possession from an item's actual, current capacities or dispositions, we render function possession irrelevant to the behavior of the functionally characterized item or the system in which it is embedded. The famous "Swampman" objection to etiological views highlights the problem. We are to imagine that a molecule for molecule duplicate of an actual person coalesces accidentally when lightning strikes swamp gas. Lacking any history of natural selection or design, Swampman's organs have no functions, according to etiological accounts, despite having identical causal profiles in all other respects to someone's organs that do have functions. The case is outlandish, but here only serves to make the more mundane point that the process that produces a product is not a causally relevant feature of that product. If Swampman has heart trouble, it makes no difference to his treatment that he lacks the evolutionary history of

homo sapiens. The problem is not specific to historical accounts. Neither our attitudes about Swampman's organs, nor the statistical norms for the organs of swamp people make a difference to Swampman's causal profile. If function possession does not depend on an item's current dispositions, it is unclear what could depend on whether the item possesses a function.

To avoid making functions epiphenomenal, we need an account that says what causally relevant information we gain from learning that an item has a given function. I will argue in Section 7 that a complete account of functional explanation reveals the historical processes emphasized by etiological accounts to be relevant to functional analysis, and therefore explanatorily important. But, that argument relies on my positive account of dysfunction from a causal role perspective. Having accepted the argument that dysfunction is rendered incoherent by a causal role account, proponents of (usually etiological) views that define function possession independently of an item's current, actual capacities argue that epiphenomenalism is the price we pay to make sense of dysfunction.¹⁰

Like deflationism about dysfunction, epiphenomenalism about functions has little to recommend it, but our philosophical theories seem to force our hand. And, like deflationism, epiphenomenalism does not cohere with the science as well as its proponents suppose. First, an item's current capacities are clearly relevant to function attributions. This is why vestigial organs like appendix have no function. Second, it is unclear why scientists would be concerned with functions if they are irrelevant to explanation. Defenders of etiological views can appeal here to the initial motivation for invoking history, that function attributions explain why an item exists. However, this justifies function attributions only in cases where we are concerned with this historical existence question for its own sake. Even in these cases, function attributions only explain an item's existence by filling in an already assumed background theory that the item was created by an intelligent designer or was favored by a process of natural selection. So, function attributions are simply an eliminable abbreviation of a historical explanation that need not invoke functions. This view cannot

explain why functional explanations are not easily eliminable, or why non-historical sciences invoke functions at all.

Defenses of etiological views typically emphasize the role of functions in categorization. It is claimed that what makes a given lump of tissue a heart is that it has the function of pumping blood. However, functions may play a less important role in categorization than fans of etiological views claim. Wings are touted as a paradigmatic case of a functional category, but the forelimbs of ostriches and flightless cormorants are called wings, despite lacking the function of enabling flight. And, some have argued that form and homology are more important for individuating hearts than function.¹¹ Insofar as functions are important to categorization it is a problem for epiphenomenalism, because the explanatory utility of functions is only vindicated if our categorization practices themselves contribute to explanation. It is mysterious how functional categories could be explanatorily useful if they do not track causally relevant properties.

We have a dilemma: The capacity to φ either is or is not necessary for having the function of φ -ing. If the first, dysfunction attributions, and all the science that relies on them, are conceptually confused. If the second, functions are epiphenomenal, and is a mystery why science invokes functions at all. Neither view is independently motivated, and both fail to capture uncontroversially successful scientific practice.

4. Three Non-Solutions

The three following views initially appear to avoid the dysfunction dilemma, but none do.

(1) Some have argued that causal role conceptions of function apply to some domains while others require a historical notion.¹² Evolutionary biologists work with a normative, historical conception of function while physiologists use a causal role conception. However, this brand of pluralism does not solve the dysfunction dilemma; it simply embraces different horns in different contexts. Non-historical sciences often make dysfunction attributions and historical sciences use

functions in causal explanations, and it is no solution to the Dysfunction Dilemma to dismiss both as conceptually confused, rather than just one.

This brand of pluralism also obscures what unifies various practices as legitimate forms of functional explanation. Compare pluralism about functions to another influential pluralist theory in philosophy of biology: Phillip Kitcher's pluralism about the species concept.¹³ When challenged to say what prevents any arbitrary concept from counting as a species concept,¹⁴ Kitcher responds that species concepts divide organisms into nested hierarchies based on biologically relevant properties.¹⁵ Kitcher has a unified conception of species, but because what is biologically relevant depends on the questions one is asking, different theoretical goals give rise to variations on the general schema. Pluralism about functions should provide a similarly principled account of the source of variation in functional explanation. While there are clearly variations in the specific practices and conceptions of functions in different fields, they are not captured by the distinction between causal role and normative (or historical) conceptions of functions.

(2) Organizational accounts have been developed specifically to avoid the epiphenomenalism of etiological accounts and still capture the normative character of functions. Organizational accounts¹⁶ begin with the observation that certain systems, for example biological systems, are self-maintaining. In a self-maintaining system an item that contributes to the maintenance of the system thereby contributes to the preconditions for its own continued existence. A heart pumping blood contributes to the circulatory system's capacity to move materials through the body. This includes bringing oxygen to the heart's own cells. Thus, the heart's contribution to the working of the larger system also explains the heart's own continued existence.

Proponents of organizational accounts argue that by tying function attributions to an analysis of a system's current capacities for self-maintenance, they avoid epiphenomenalism. They also claim that contributions to self-maintenance answer the existence questions emphasized by

etiologically, and thus capture the normativity of functions. Contribution to self-maintenance is an alternative to evolutionary history, statistics, or human desires for isolating a non-arbitrary norm. But, as argued in the previous section, any account of the norm relative to which an item counts as dysfunctional is compatible with accepting or denying that being capable of φ -ing is a necessary condition for possessing the function of φ -ing, and it is this choice which leads to one horn or the other of the Dysfunction Dilemma. The dilemma thus arises as forcefully for organizational accounts as for other options already considered. However, all of these accounts of functional norms, including the organizational account, are compatible with the solution I defend.

(3) According to Bence Nanay, function attributions have modal—here read, counterfactual—force. Nanay argues that for an item to have the function of φ -ing is for it to be the case that φ -ing contributes to survival and reproduction (or some other “goal”) in a relatively close possible world, and that there are no closer worlds where φ -ing does not so contribute.¹⁷

Possible worlds semantics are a standard linguistic tool for capturing discourse about norms, so it is little surprise that the modal account allows for a notion of dysfunction. If an item is dysfunctional, it is unable to φ in the actual world, but this does not rule out there being some nearby possible world in which φ -ing contributes to survival and reproduction with no even closer world in which it does not. The modal view can thus accommodate cases where an item is unable to perform its function.

The interesting question is whether Nanay’s account avoids epiphenomenalism. Nanay explicitly notes that his definition is intended to make an item’s function depend only on intrinsic features of the functionally characterized item.¹⁸ Presumably those features would be causally relevant. Unfortunately, Nanay does not say what those features might be. As a semantic theory, this is acceptable. Linguists standardly bracket questions about what the “ordering source” in their possible world models correspond to in reality. But, our question is what functions are, not how to

give a formal semantics for function-talk. Possible worlds semantics would apply just as well if the ordering source is human expectations, statistical norms, histories of selection, or any other relation to a norm. Modal semantics is compatible with any theory of functions, and the assertion that the ordering on worlds reflects causally relevant features of functionally characterized items presupposes a solution to the Dysfunction Dilemma but does not provide one.

5. Where the Function Debate Went Wrong

We seem caught between painting functions as non-normative or as non-explanatory, and both options fail to do justice to successful scientific practice. I have foreshadowed that the way out of the Dilemma is to reject the argument in Section 2 that Cummins's definition of functions renders dysfunction attributions incoherent. To illustrate the problem with that argument, I offer a parallel argument that curing heart failure is conceptually incoherent.

Heart failure is characterized by the inability of the heart to pump blood at the rate needed to sustain metabolizing tissues, or the ability to do so only at an elevated filling pressure.¹⁹ For simplicity, call the ratio of heart rate to filling pressure efficiency, and denote the efficiency required to sustain metabolizing tissue by ' E '. So, a failing heart is one incapable of pumping at E . However, if a given failing is curable, it is possible to make it pump at E again. But, an item cannot be made to do something it is not capable of doing, so a curable heart is capable of pumping at E . Therefore, a curable failing heart both is and is not capable of pumping at E , which is absurd, so the very idea of curing heart failure is conceptually incoherent.

We would rightly scoff at this argument. It relies on an equivocation. When a doctor says that a failing heart is curable, she means that it is capable of pumping at E given certain interventions like diet, exercise, medication, and surgery. However, when that same doctor diagnoses the heart as failing, the point is that the heart is incapable of pumping at E without those

interventions. There is more than one capacity to pump at E at issue, and there is nothing absurd about the same heart having one and lacking the other.

The argument that causal role conceptions of function render dysfunction attributions incoherent relies on the same equivocation. For an item's capacity to φ to be its contribution to the capacities of a system, that item must be capable of φ -ing. But, being dysfunctional does not require that an item be incapable of φ -ing without qualification, only that it be incapable of φ -ing under some specified set of normal circumstances. Heart failure is classed as a dysfunction because hearts have the function of pumping at E , and a failing heart cannot. However, this does not mean that a failing heart is incapable of ever, under any circumstances, pumping at E , only that it cannot do so without specific interventions like diet, exercise, medication, and surgery.

Furthermore, that a failing heart is unable to pump at E under conditions in which a healthy heart could does not render the failing heart's capacity to pump irrelevant to the capacities of the circulatory system as a whole. Heart failure is a problem precisely because the capacity of the system as a whole to transport material through the body at sufficient efficiency to sustain metabolizing tissue depends on the heart's capacity to pump at E . The capacity of a circulatory system (\mathcal{S}) to transport materials efficiently (ψ) is partially explained by the capacity of the heart (x) to pump efficiently (φ) for both failing and healthy hearts despite differences in the circumstances under which these capacities would manifest.

This example suggests the following picture: Function attributions express that there is an explanatory relation between the capacity of the functionally characterized item to φ and the capacity of a system to ψ . But, function attributions are neutral about which capacity to φ the functionally characterized item has—that is, under which particular circumstances it would φ . Given the dependence of the system's capacity to ψ on the item's capacity to φ , it is useful to know under what

conditions the item would φ , so it is useful to track which capacity to φ it has. I will argue that dysfunction attributions allow us to do just this.

6. Dysfunction in Functional Analysis: A Simplified Model

Developing a complete account of functions along the lines suggested in the previous section is a large project. Here I will offer a proof of concept through a simplified model. Like all models, this one will trade nuance for precision. The goal is not to provide a formal theory immune to all counterexamples but rather a precise characterization of the simplest kinds of cases as an indication of how a more developed theory would look.

Functional analyses explain one disposition by decomposing it into others, organized in a particular way—note that capacities can be treated as a special case of dispositions. Little has been said about the relevant sense of ‘organization.’ Cummins says only that it can be represented by a program or flowchart. More recently, several philosophers have argued that an adequate functional analysis must delineate mechanisms.²⁰ However, the link between functions and mechanisms is controversial, largely because it is controversial how best to explicate the notion of mechanism itself.²¹ Fortunately, we can give a broad characterization of the relevant sense of organization without settling these issues by using counterfactual conditionals as proxies for dispositions.

To a first approximation, an item has a disposition to φ just in case it would φ under a given set of circumstances. In the literature on the metaphysics and semantics of dispositions, it is controversial whether this simple formula is adequate, but the goal here is not to provide a metaphysical or semantic account of dispositions. It is to show how functional analysis works, and for that purpose, the formula will serve well.

Dispositions have three important structural features. A disposition has a *manifestation*, φ . The heart's disposition to pump blood is manifested in the heart's pumping blood, and solubility is manifested in the dissolution of the soluble substance. The disposition also has a set of *triggering*

conditions under which the manifestation would occur. A heart pumps blood when there is blood present to be pumped, when the brain is sending electrical impulses to the heart, and when it is at standard Earth temperature and pressure, and so on. In practice, many of these conditions are assumed to be fixed, and scientists do not pay attention to them. Call the conditions we ignore for practical purposes the *background conditions*.

Finally, dispositions have a set of *basis conditions*, the conditions that must be satisfied for an item to possess the disposition, and in virtue of which the triggering conditions give rise to the manifestation. Water-soluble materials have the disposition to dissolve in water. The triggering condition, being in water, leads to the manifestation, dissolving, because the soluble item has particular molecular properties like molecular polarity. Having a certain level of molecular polarity is thus a basis condition for being water-soluble. Possessing a particular contractile strength is a basis condition for a heart to have the capacity to pump efficiently given a particular set of triggering conditions.

Basis conditions need not be internal or intrinsic to an item. One basis condition for having the capacity to pass the salt is being located sufficiently close to the salt. Similarly, triggering conditions need not be external or extrinsic to an item. Most of us are disposed to seek food when we are hungry. Hunger is an internal triggering condition.

If an item has a given disposition (or capacity), then there is some (possibly very long and hard to generate) counterfactual conditional of the following form that is true of it:

(Background Conditions & Triggering Conditions & Basis Conditions) → Manifestation

Listing the conditionals corresponding to the capacities in a functional analysis generates a partial flowchart-like structure with the conditional arrows linking triggering conditions to manifestations. The figure below demonstrates this point using the circulatory system. Background conditions are omitted, and basis conditions are left unspecified.

The arrows making up the path correspond to explanatory relations, so the flowchart specifies an explanatory connection in virtue of which the triggering conditions of the analyzed disposition give rise to its manifestation. The flowchart thus constitutes a specification of the basis conditions of the disposition targeted by the analysis.

A path on a flowchart is only a very loose characterization, and a full theory of adequacy conditions on an analytical account would specify characteristics the path must satisfy to be explanatory. Recent work on the nature of mechanisms, and scientific explanation more generally, provides a wealth of options for a more precise characterization. However, the present loose characterization is sufficient to show that a single functional analysis can explain the capacities of a whole class of systems with a range of distinct but systematically related capacities.

The notion of systematically related capacities can be modeled using equivalence classes. For any two dispositions D_1 and D_2 , D_1 is equivalent to (or, in the same equivalence class as) D_2 if and only if the union of the sets of basis and triggering conditions for D_1 is identical to the union of the sets of basis and triggering conditions for D_2 , and the manifestations of D_1 and D_2 are the same. Whether two dispositions are in an equivalence class is relative to a list of conditions, so to model real cases conditions must be specified carefully. Medication and surgery are not among the basis or triggering conditions for the capacity of a healthy heart to pump at E , but they may be for a failing heart. However, these interventions on a failing heart aim to restore a particular ratio of heart strength to blood pressure, which is a basis condition for the capacity of healthy hearts to pump at E . Failing hearts have the capacity to pump at E that differs from the capacity of a healthy heart to do so only in that the ratio of heart strength to blood pressure being in a given range, is a triggering rather than a basis condition. Thus, the capacities of failing and healthy hearts to pump at E are in an equivalence class.

Scientists move fluidly between treating a given condition as a triggering or as a basis condition, as when a doctor moves from diagnosing heart failure to discussing treatment. In the diagnostic context, that the ratio of heart strength to blood pressure is within a specified range is treated as a basis condition, either satisfied or not, but once it is determined that this condition is not satisfied the relevant question becomes how best to satisfy it. In the new context of treatment, the ratio of heart strength to blood pressure is treated as a triggering condition, as something to be manipulated. This shift alters which disposition within an equivalence class is contextually salient.

Much of the explanatory power of a functional analysis arises from the possibility of iterating functional analyses. In the analysis depicted above, the details of how hearts work are left as unspecified basis conditions for the heart's capacity to pump blood. However, those basis conditions form part of the explanatory chain represented by the flow chart. For many purposes they can be "black-boxed"—to borrow terminology from Carl Craver and Lindley Darden²²—but, treating one of those conditions as a triggering condition requires us to bring it and its relations to other conditions to the fore. Shifting between treating the same condition in the same functional analysis as a basis or triggering condition—that is, focusing on a different disposition within an equivalence class—serves to highlight the causal relations relevant to the explanatory task at hand.

A functional analysis specifies an abstract structure of explanatory relations between conditions, by grouping those relations into dispositions. Function attributions specify an item's causal role in a system by placing the manifestation of one of its dispositions in this network. That manifestation will have various *input conditions*—that is, triggering and basis conditions. To possess the function of φ -ing, an item must be such that it would φ if all of those input conditions were satisfied. Otherwise, the requirement that an explanatory path be traceable from the triggering conditions to the manifestation of the analyzed capacity would be violated. Hearts and bellows can both pump blood, but only the former would do so under the relevant input conditions. But, the

abstract causal structure, and the place of an item's capacity to φ within it, does not depend on a particular division of the input conditions into triggering and basis conditions, or on any input conditions actually being satisfied. Therefore, function attributions are neutral about which capacity to φ an item has, as long as that capacity is in the relevant equivalence class. Both healthy and failing hearts have the function of pumping at E .

Just as we can describe the location of a point in space with reference to an arbitrarily chosen point of reference and a unit of distance, using a system of coordinates, we can locate an item's capacity within an equivalence class given an arbitrarily chosen privileged capacity. Dysfunction attributions do just that. We can model the way this works by defining an ordering on the equivalence class. Dispositions D_1 and D_2 in equivalence class $[D]$ are such that $D_1 < D_2$ if and only if the set of triggering conditions for D_1 is a superset of the set of triggering conditions for D_2 . Let D^* be the privileged capacity in $[D]$. Then an item is dysfunctional if it possesses the function of φ -ing and its greatest capacity to φ in $[D]$ is less than D^* . According to this model, a failing heart is dysfunctional because the triggering conditions for its capacity to φ include the set of normal circumstances—the triggering conditions for the privileged capacity—plus the condition that the ratio of heart strength to blood pressure be within a particular range, which is a basis condition for the privileged capacity. The intuitive idea behind this definition is that one must satisfy more conditions, or do more work, to get a dysfunctional item to perform its function.

That a failing heart cannot pump at E under normal circumstances, and therefore lacks the privileged capacity, is interesting precisely because it has the function of pumping at E . If it did not have the function of pumping at E , it would not make a difference to the larger system whether it could do so under a particular set of circumstances. Given that it does have that function, it is useful to know the conditions under which it would pump at E because this knowledge allows for manipulations of the system as a whole through manipulations of those conditions, in this case

through medication, exercise, diet, and surgery. Far from mere loose talk or an eliminable abbreviation, dysfunction attributions facilitate reasoning and communication about how to manipulate complex systems by providing more fine-grained causally relevant information than function attributions alone.

7. Norms and Natural Kinds

Many open questions remain. The model in the last section sacrificed nuance for precision, and some indication of how the idealized model meets practice is owed. First, the equivalence classes in the model are relative to a list conditions and can be gerrymandered arbitrarily. A principled account of the scope of functional analyses in practice is needed. Second, though the explanatory strategy sketched in the last section can rely on any arbitrarily chosen norm, represented by the privileged capacity, dysfunction attributions do not appear arbitrary, so how the norm is determined in an explanatory context requires explanation. Finally, my account may be open to the standard objection to Cummins's original account that it is too permissive, licensing function (and now dysfunction) attributions not sanctioned in practice.

The answer to all three questions is that the nature of the kinds studied in a given research project guide the scope of function attributions, the choice of norm, and the domain to which functional analysis properly applies. Function attributions are typical of scientific claims in that they are generic claims about kinds of things. Physiologists do not merely claim that individual hearts that have been examined have the function of pumping blood, but that hearts in general have that function, despite the fact that no physiologist will ever examine the vast majority of them. Thus, function attributions, like all scientific generalizations, must be projected from a small number of examined cases to the entirety of the kind they instance.

A kind is natural to the extent that it permits generalizations to unexamined instances. When we make functional claims about a kind of system, we rely on the fact that we can reliably depend on

natural kinds to share many features, and we can tell which features are the ones likely to be shared. We can do this because the fact that these features are shared is no accident; there are underlying mechanisms that explain why instances of the kind tend to share particular kinds of features in common.²³ Richard Boyd has called these “homeostatic mechanisms” while Ulrich Krohs dubs them “type fixing processes.”²⁴ I will call them unifying mechanisms, with the proviso that I intend the term ‘mechanism’ in the loose, scientific vernacular sense, without assuming any particular explication of mechanisms from the recent literature in philosophy of science.

Thanks to unifying mechanisms, instances of a natural kind tend to have similar capacities. This licenses generalizations about hearts in light of data about particular hearts. Thus, the scope of a functional analysis is usually, like most scientific generalizations, over a natural kind. And it is often most useful to choose a norm around which instances of the kind non-accidentally tend to cluster. Shared developmental and evolutionary history, plus shared environmental embedding, cause hearts to non-accidentally approximate the system we represent in physiology textbooks, though always imperfectly. This idealized system is an abstraction from a messy world, but it serves as a particularly useful descriptive point of reference for real systems. Design plans serve a similar role for artifacts.

In sciences like medicine and conservation biology the overarching goal is to cause target systems to align with a certain ideal. Insofar as target systems come to (or continue to) exhibit the relevant feature, it will be no accident, because we are introducing a new unifying mechanism, namely human intervention. Thus, social norms and human desires can serve as useful norms even in cases where human activity does not explain much of the current similarity of the target kinds.

Statistical norms may serve well when unifying mechanisms are unknown or difficult to detect directly, but I suspect statistical views of dysfunction put the cart before the horse. In most fields statistical norms are only useful insofar as they indicate something about the unifying mechanisms. For example, assuming that a population is most likely to be at or near a local fitness

maximum with respect to an arbitrarily chosen parameter, statistical norms can be a good indicator of what has been favored by natural selection.

Only certain kinds of mechanisms are capable of generating systems with the kind of complex hierarchical structure that makes functional analysis an attractive explanatory tool, or the clustering of capacities around a norm that makes dysfunction attributions useful. We find it odd to ascribe functions to systems that are not the end result of natural selection or design, including those studied in the physical sciences, because such systems will not reliably possess the sorts of capacities we need functional analysis to explain. We sometimes do functionally analyze the capacities and dispositions of individual systems: The earth's capacity to sustain life is explained by its capacity to support liquid water, its disposition to maintain a stable axis of rotation, its capacity to deflect incoming radiation, and so on. From the perspective of explaining how Earth can sustain life, the moon serves the function of stabilizing Earth's rotational axis, thereby preventing rapid climate fluctuation, but we do not say that the moon possesses this function because the moon serves this function accidentally. That is, the moon is not an instance of a kind with unifying mechanisms that cause it to play this causal role in sustaining life. Functional analysis only or almost only applies to items with a particular kind of history because only or almost only kinds with a particular sort of history will non-accidentally share the sort of complex, hierarchically organized causal features functional analysis explains.

8. Conclusion

Extant accounts of function have foundered on the Dysfunction Dilemma:

- **Choice:** Either (A) Being capable of φ -ing either is a necessary condition for possessing the function of φ -ing, or (B) Being capable of φ -ing either is not a necessary condition for possessing the function of φ -ing.

- **Horn 1:** If \mathcal{A} , then dysfunction attributions are incoherent, and much apparently good science emerges as conceptually confused.
- **Horn 2:** If \mathcal{B} , then functions are causally and explanatorily inert (epiphenomenal), and much apparently good science emerges as explanatorily empty.
- **Dilemma:** Either way, our philosophical account of functions is at odds with uncontroversially successful scientific practices.

But, the first horn of the dilemma arises from an argument that equivocates between having a capacity to φ that causally contributes to a system and having the specific capacity to φ under a particular set of privileged circumstances. Using this distinction, I have developed a simplified model that shows how dysfunction attributions can be not only coherent on a causal role approach but contribute to functional analysis by providing finer grained causal information than function attributions alone. I have suggested that this model can be connected to practice by attending to the mechanisms that unify the natural kinds to which functional analyses apply, and that my account vindicates the insights of etiological accounts. The account thus unifies the theory of functions in addition to dissolving the Dysfunction Dilemma.

Notes

¹ Christopher Boorse, "Health as a Theoretical Concept," *Philosophy of Science*, 44, 2 (December 1977): 542-573; Jerome C. Wakefield, "The Concept of Mental Disorder," *American Psychologist*, 47, 3 (March 1992): 373-388.

² Ruth G. Millikan, *Language, Thought, and Other Biological Categories: New Foundations for Realism* (Cambridge MA: MIT Press, 1984); Ruth G. Millikan, "Biosemantics," *The Journal of Philosophy*, 86, 6 (June 1989): 281-297; Fred Dretske, *Explaining Behavior: Reasons in a World of Causes* (Cambridge MA: MIT Press, 1988); Karen Neander, "Misrepresenting and Malfunctioning," *Philosophical Studies: An International Journal for Philosophy in the Analytic Tradition*, 79, 2 (August 1995): 109-141; John Maynard-Smith, "The Concept of Information in Biology," *Philosophy of Science*, 67, 2 (June 2000): 177-194.

³ Robert Cummins, "Functional Analysis," *The Journal of Philosophy*, 72, 20 (November 1975): 741-765; Robert Cummins, *The Nature of Psychological Explanation* (Cambridge MA: MIT Press, 1983).

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- ⁴ Cummins, "Functional Analysis," *op. cit.*; Paul S. Davies, *Norms of Nature: Naturalism and the Nature of Functions* (Cambridge MA: MIT Press, 2001); Ruth G. Millikan, "In Defense of Proper Functions," *Philosophy of Science*, 56, 2 (June 1989): 288-302. Karen Neander, "Functions as Selected Effects: The Conceptual Analyst's Defense," *Philosophy of Science*, 58, 2 (June 1991): 168-184.
- ⁵ Paul E. Griffiths, "Functional Analysis and Proper Functions" *The British Journal for the Philosophy of Science*, 44, 3 (September 1993): 409-422; Denis M. Walsh and André Ariew, "A Taxonomy of Functions," *Canadian Journal of Philosophy*, 26, 4 (December 1996): 493-514; Matteo Mossio, Christian Saborido, and Alvaro Moreno, "An Organizational Account of Biological Functions," *The British Journal for the Philosophy of Science*, 60, 4 (December 2009): 814-831.
- ⁶ Boorse, "Health as a Theoretical Concept," *op. cit.*
- ⁷ Davies, *Norms of Nature*, *op. cit.*
- ⁸ Jack W. Bradbury and Sandra L. Vehrencamp, *Principles of Animal Communication*, 2nd ed., (Sunderland MA: Sinauer Associates, 2011).
- ⁹ See especially, Millikan, *Language, Thought, and Other Biological Categories*, *op. cit.* and Neander, "Functions as Selected Effects," *op. cit.*
- ¹⁰ Dretske, *Explaining Behavior*, *op. cit.*; Ruth G. Millikan, "An Input Condition for Teleosemantics? Reply to Shea (and Godfrey-Smith)," *Philosophy and Phenomenological Research*, LXXV, 2 (September 2007): 436-455; Karen Neander, "The Narrow and the Normative," Unpublished, cited with permission: <http://www.nyu.edu/gsas/dept/philo/courses/content/papers/neander.pdf> (last accessed, 5/14/18)
- ¹¹ Berent Engç, "Function Attributions and Functional Explanations," *Philosophy of Science*, 46, 3 (September 1979): 343-365; Ron Amundson and George Lauder, "Function Without Purpose: The Uses of Causal Role Function in Evolutionary Biology," *Biology and Philosophy*, 9, 4 (October 1994): 443-469; Paul E. Griffiths, "Function, Homology, and Character Individuation," *Philosophy of Science*, 73, 1 (January 2006): 1-25.
- ¹² See especially, Peter Godfrey-Smith, "Functions: Consensus Without Unity," *Pacific Philosophical Quarterly*, 74, 3 (September 1993): 196-208.
- ¹³ Philip Kitcher, "Species," *Philosophy of Science*, 51,2 (June 1984): 308-333.
- ¹⁴ Elliot Sober, "Sets, Species, and Evolution: Comments on Philip Kitcher's "Species"," *Philosophy of Science*, 51, 2 (June 1984): 334-341.
- ¹⁵ Philip Kitcher, "Against the Monism of the Moment: A Reply to Elliot Sober," *Philosophy of Science*, 51, 4 (December 1984): 616-630.
- ¹⁶ Mossio, Saborido, and Moreno, "An Organizational Account of Biological Functions," *op. cit.*
- ¹⁷ Bence Nanay, "A Modal Theory of Function," *The Journal of Philosophy*, 107, 8 (August 2010): 412-431.

¹⁸ *Ibid.*

¹⁹ Douglas P. Zipes *et al.*, eds., *Braunwald's Heart Disease: A Textbook of Cardiovascular Medicine*, 7th ed., Vol 1, (Philadelphia: Elsevier, 2005).

²⁰ Carl F. Craver, "Role Functions, Mechanisms, and Heirarchy," *Philosophy of Science*, 68, 1 (March 2001): 53-74; Davies, *Norms of Nature*, *op. cit.*; Gualtiero Piccinini and Carl Craver, "Integrating Psychology and Neuroscience: Functional Analyses as Mechanisms Sketches," *Synthese*, 183, 3 (December 2011): 283-311.

²¹ For example, Daniel Weiskopf, "Models and Mechanisms in Psychological Explanation," *Synthese*, 183, 3 (December 2011): 313-338.

²² Carl F. Craver and Lindley Darden, *In Search of Mechanisms: Discovery Across the Life Sciences*, (Chicago: University of Chicago Press, 2013).

²³ Richard Boyd, "Homeostasis, Species, and Higher Taxa" in Robert Wilson, ed., *Species: new Interdisciplinary Essays* (Cambridge MA, MIT Press, 1999): pp. 141-185.

²⁴ Ulrich Krohs, "Functions as Based on a Concept of General Design," *Synthese*, 166, 1, (January 2009): 69-89.

Chapter 2: Do Genes Have Intentionality?

1. Introduction

Biologists regularly use representational notions to describe genes. Talk of genetic codes, information, blueprints, messages, programs, recipes and the like are commonplace. Recently, there has been debate about the theoretical significance of this talk. Though a few philosophers and biologists have offered positive accounts of genetic intentionality,¹ by and large the response has been deflationary or critical, with some arguing that representational notions are eliminable² or metaphorical,³ and others arguing that they are erroneous and misleading.⁴ Here I will defend the idea that genes have intentionality—that is, semantic or representational content.

Rather than attempting to answer individual objections piecemeal, I divide the problems facing an account of genetic intentionality into three general issues: 1) Genetic intentionality is causally and/or explanatorily inert. 2) Genetic intentionality encourages tendencies toward genetic determinism by making gene action seem context insensitive. 3) Details about genetic mechanisms reveal them not to be representational. First, I argue that while most of the literature on genetic intentionality has focused on one motivation for thinking of genes representationally—the arbitrary code-like mapping of nucleotide triplets to amino acids—there is a more powerful motivation, exemplified by Ernst Mayr's defense of genetic programs.⁵ Mayr's motivations for thinking of the genome as a program parallels the standard argument for computational theories of mind that only a representational theory can explain the end-directed nature of certain processes. Given this particular view of the explanatory role of genetic intentionality, I argue that the main objections and challenges to the idea that genes have a semantics are parallel to those facing representational theories of mind, and I suggest parallel responses to those challenges. I do not attempt to defend representational theories of mind or suggest that genetic intentionality and representational theories

of mind stand or fall together, but the parallel should render genetic intentionality considerably more plausible.

2. No Work for a Theory of Genetic Intentionality?

Philosophical work on the idea that genes have semantic properties is motivated by the common biological practice of applying informational and representational concepts to genes. Biologists have tended to assume that these notions are theoretically well founded by information theory and computer science, but there has been general consensus among philosophers that the ways in which biologists have used these concepts appear to rely on semantic concepts not explicated by the mathematical theories of information and computation. Information theory⁶ in mathematics concerns the amount of information that can be transmitted over a channel from a sender to a receiver, but it is silent about what, if anything, is the content of the message. As Carl Bergstrom and Martin Rosvall⁷ have argued, information theory plays an important role in biological work on the transmission of inherited information. But, biologists care about the transmission of information precisely because it is supposed to code for or represent phenotypic features of the organism. That is, inherited information is not just the structure of uninterpreted strings of amino acids; rather, genes are conceived of as carriers of semantic information that is interpreted, not only by biologists, but by the developmental system itself.

Paul Grice⁸ and Fred Dretske⁹ have developed a notion of meaning as causally mediated correlation that can be appended to the concept of information provided by information theory, but this notion of correlational information is also not enough to capture the sense in which genes are supposed to represent phenotypic traits. This sense of information captures the sense in which smoke means fire and the number of rings in a log represent the age of the tree. This kind of representation plays a role in biological theory and practice; however, correlational information alone does not provide a full foundation for the use of representational concepts in genetics. A gene

for trait X remains a gene for trait X , even if due to unusual environmental conditions the organism does not have trait X . In the correlational sense of information, a failure of correlation is a failure to represent. If some climatic anomaly causes a given tree's number of rings to not correlate with its age in the usual way, then the number of rings simply fails to represent or carry information about the tree's age. Genetics programs, codes, blueprints, and so on can misrepresent, in the sense that the trait coded for may not in fact develop, but correlational information cannot capture the possibility of misrepresentation. Thus, biologists appear to presume that genes can carry semantic information, or more theoretically neutrally, semantic content, similarly to natural languages and conceptual cognition. Recent debate has been largely concerned with the cogency of the idea that genes have semantic content or intentionality.

Phillip Kitcher has claimed that talk of “coding” is a rhetorical flourish that does no theoretical work, and several philosophers have argued that representational notions applied to genes are useful but merely heuristic or metaphorical.¹⁰ Peter Godfrey-Smith has defended the claim that genes literally semantically code for protein sequences, but denies that there is any useful theoretical sense in which they code for or represent phenotypic traits.¹¹

Negative universals are difficult to establish, so these arguments tend to take the form of debunking genealogies of the source of the idea that genes code for traits. Both Sahotra Sarkar and Peter Godfrey-Smith trace the origins of talk of genetic coding or representation to early work, especially by Watson and Crick, on the structure of DNA. In short, analogies with computers and coding systems like Morse code aided in the discovery of the mapping of nucleotide triplets to the amino acids that make up proteins, and like the mapping between any bit of language or code and its meaning, the mapping between nucleotide triplets and amino acids is in an important sense arbitrary.¹² This success seemed to support a more general picture of the genome as a program or set of instructions for building the organism. But, Godfrey-Smith claims that beyond this original

context, there is no useful explanatory work for genetic intentionality, and others question whether it does any real work, even in that original context.¹³

There are important questions about the role of representational notions in molecular biology and genetics proper, and about whether these initial motivations for using representational notions in those fields support the application of representational concepts to genes in other fields like developmental biology and evolutionary biology, but I will largely sidestep these issues and focus on an alternative line of argument for genetic intentionality that has not received much attention. Though biologists were initially motivated by mechanistic analogies between digital computers and the way DNA codes for proteins, I will argue that Ernst Mayr, an evolutionary biologist who also wrote extensively on the history and philosophy of biology, has developed a more promising motivation.

As Alexandre Peluffo has recently argued, Mayr developed his conception of genetic programs in conversations with molecular biologist Jacob Monod.¹⁴ Mayr took himself to be simply reporting the findings of molecular biologists when he claimed that genes instantiate a program. However, the notion of genetic programs plays a central role in Mayr's philosophical and historical work, and perhaps unwittingly, he develops an independent rationale for attributing intentionality to genes, independent of the mechanistic considerations that motivated molecular biologists to adopt 'coding' talk. For Mayr, the genetic program provides a naturalistic version of Aristotle's notion of final causation, at least for certain kinds of systems.

The role of final causes, or teleology, in biology has long a source of controversy. On the one hand, biologists appear to rely heavily on teleological language, often referring to the goal or function of a given trait. But, according to standard conceptions of scientific progress, the scientific revolution marked a turn away from teleology. Physics succeeded by eschewing teleology in favor of what Aristotle called "efficient causes," and what we now just call "causes." With the abandonment

of teleology taken to be a mark of real science, it seems biology was faced with giving up talk of ends, purposes, and functions, or showing that they are merely rhetorical and do no explanatory work. As part of a general defense of the autonomy of evolutionary biology in the face of claims that real science must all reduce to physics—or at least real biology must reduce to molecular biology—Mayr argued that teleological language is essential to biology and cannot be captured in the vocabulary of the physical sciences. The teleological nature of explanations in evolutionary biology block reductionism. However, this left Mayr in need of a story about how teleology could be scientifically respectable. He pursued a divide and conquer strategy, arguing that phenomena that had previously be classed as teleological were heterogeneous and required different explanatory strategies. One class of such phenomena, he dubbed ‘teleonomic.’ Teleonomic processes he defined as those under the control of a program. Unlike molecular biologists who were inspired by the mechanisms underlying digital computers, Mayr was impressed by a computer’s ability to engage in end-directed processes through those well understood physical mechanisms.

“mechanisms exist which instantiate, i.e. “cause” this goal-seeking behavior. ...

Someone might claim that the difficulties of an acceptable definition for teleological language in biology had simply been transferred to the term program. This is not a legitimate objection because it fails to recognize that, regardless of its particular definition, a program is (1) something material, and (2) it exists prior to the instantiation of the [goal-directed] process. Hence, it is consistent with a causal explanation. ... Tentatively, a program might be defined as coded or prearranged information that controls a process (or behavior) leading it toward a given end”¹⁵

Mayr is simply noting that we need not have a precise definition of a program in hand to know how computers are able to non-mysteriously produce goal-directed behaviors. We informally talk as if a program “tells” a computer what to do, but the computer works because various physical

items are so arranged inside of it so that their causal relations map onto the steps in an algorithm as expressed in a language,¹⁶ though it is not fully settled what exactly the nature of this mapping is, for example whether it consists in something more than mere correlation.¹⁷ This mapping, that philosophers, linguists, computer scientists, and psychologists would call a semantics, Mayr refers to as “prearranged information.” Mayr’s central point is that we need not posit an immaterial “vital essence”. The theory of computation already shows that goal-directed processes can be explained by a certain kind of causal mechanism. Defining the notion of a program precisely is the kind of formal filling in that can come later.

It is worth noting that while Mayr was certainly influenced by Monod, he departs from Monod in an important way. Monod defends a cybernetic notion of information. The cybernetic tradition defines a goal as an end state to which a system converges from many starting configurations, adjusting homeostatically to perturbations in its trajectory to that endstate.¹⁸ However, Mayr argues that this definition does not single out the phenomena of interest since it would make the tendency of rivers to flow into the sea, of bodies on earth to fall to the ground, and the overall increase in entropy in a closed system count as goal-directed activities. The cyberneticists emphasize the role of feedback mechanisms that correct deviations from approaching the relevant end-state, so they may not find this objection convincing, since many of the processes Mayr cites lack these mechanisms. But, Mayr notes claims that these feedback processes, while important, “are not the essence of teleonomic activity.”¹⁹ Rather, it is that “mechanisms exist which initiate, i.e. ‘cause’ this goal-seeking behavior.”²⁰ Here I am not concerned with the cogency of Mayr’s critiques or with the details of the cybernetic account. I suspect Sahotra Sarkar is right that the cybernetic notion of information has not been theoretically fruitful,²¹ but the important point for now is that Mayr’s argument is not a version of the cybernetic view despite influence from Monod. Rather,

Mayr's argument is, in essence, the same argument motivating computational and representational theories of mind.

For the sake of comparison, consider the following retrospective summary of the case for the representational theory of mind, authored by Jerry Fodor.

“Cognitive science is fundamentally concerned with a certain mind-world relation; the goal is to understand how its mental processes can cause a creature to behave in ways which, in normal circumstances, reliably comport with its utilities. There is, at present, almost universal agreement that theories of this relation must posit mental states some of whose properties are representational, and some of whose properties are causal. The representational (or, as I'll often say, semantic) properties of a creature's mental states are supposed to be sensitive to, and hence to carry information about, the character of its environment. The causal properties of a creature's mental states are supposed to determine the course of its mental processes, and eventually, the character of its behavior. Mental entities that exhibit both semantic and causal properties are generically called 'mental representations', and theories that propose to account for the adaptivity of behavior by reference to the semantic and causal properties of mental representations are called 'representational theories of mind'.”²²

A utility is a kind of end, and cognitive science is in the business of explaining how cognition brings it about that behavior is reliably directed at this end. Though cognitive science is also concerned to explain various kinds of failure—Oedipus marrying his mother being a case on which philosophers in particular tend to fixate—these cases are only interesting against the backdrop of general success, and in any case what it means to explain failures is unintelligible absent a given end which a creature might fail to realize. Note that Fodor, like Mayr, isolates two features which

computational processes have, semantic content (Mayr's "pre-arranged information") and causal efficacy. In both cases, the idea is that a semantic mapping of features of the world onto representations with causal relations that map onto semantic relations allow computers to non-mysteriously engage in end-directed processes.

The defining insight of cognitive science is that computation can explain the end-directedness of behavior non-mysteriously. And there is, as Fodor notes, "near universal" agreement that computation involves physical (and thus causally efficacious) items which have semantic properties or "carry information." However, the minority who disagree have been vocal, and even among the representationalists, controversy abounds about the details. Representational theories face a host of problems, but also to many appear to be, as Fodor puts it, "the only game in town."²³ The result has been decades of literature spelling out options for solving the various theoretical puzzles associated with the central insight. But, with the parallel between Mayr's and Fodor's case for invoking semantic properties in view, the debate about representational theories of mind proves to be instructive about the theoretical options for dealing with parallel problems in the case of genetic intentionality.

3. Problem 1: Causal Inertness

Because there is no widely accepted theory of intentionality it can be difficult to assess whether genes have it. A failure to meet a particular definition could mean that genes do not have intentionality, or it could mean that the assumed theory of intentionality is mistaken. As long as the case for genetic intentionality rests only on structural analogies between genes and computers or language, this is an especially pressing problem, but Mayr's case does better here. Representational theories of mind enjoy widespread—according to Fodor, "near universal"—support despite the lack of a generally accepted theory of intentionality. Representational theories appear to be the only option for doing the required explanatory work, so its supporters assume there must be a workable

theory of intentionality that does the job and are currently engaged in developing it. There are those who question whether representationalism is really the only game in town,²⁴ but this is a problem with representational theories generally, not a problem specific to genes. So, I will assume for the sake of argument that representationalism about the mind is correct. Given that development, behavior, and other biological phenomena are goal-directed in the relevant sense—and, cognition strikes me as just a special case of this—then, we have the same reasons to adopt a representational theory in these other cases. It is worth noting that this does not directly imply that the representations are specifically *genetic*, but for simplicity I will continue to focus on genes and address the questions of why we would isolate genes as the carriers of intentionality in a later section. With parallel motivations, the lack of a ready at hand general theory of intentionality does not undermine the case for treating genes as intentional. In fact, it puts the onus on a plausible theory of intentionality to capture genetic intentionality in addition to the standard explanatory targets, natural language and conceptual cognition.

There are a number of theoretical options for providing an account of intentionality, but the literature on genetic intentionality has focused on one particular option: teleosemantics. According to the teleosemantic account, an item's representational content is determined by a history of selection.²⁵ Semantic accounts that rely on mapping or carrying information face difficulties accounting for the possibility of misrepresentation because, as in the example of tree rings above, an item that fails to carry information about or map onto a particular item simply does not represent it. Teleosemantics says that an item represents or denotes a given referent if it has the function of carrying information about or mapping onto it. Since it is possible for an item to fail to perform its function, it is possible for an item to misrepresent by failing to map onto or carry information about that which it has the function of mapping onto or carrying information about. Having a function,

according to teleosemantics, means having a history of selection. An item has the function of mapping onto or carrying information about a referent if that item was selected to do so.

However, teleosemantics faces a number of problems, and one in particular has led many to reject genetic intentionality. It appears to render representations explanatorily inert, or at least to render them unable to do the explanatory work genetic intentionality is supposed to do. By painting semantic content as wholly a reflection of an item's history of selection, teleosemantics also paints explanations that invoke representations as historical explanations.²⁶ But, computational/representational notions are supposed to provide a non-mysterious causal mechanism for goal-directedness. Natural selection explains how goal-directed systems can come to exist, given that they are not likely to arise by chance, but it does not explain how the system actually engages in goal-directed activities. Teleosemantics misses the explanatory target because it links semantic content to the process that explains how goal directed systems come to exist rather than to the features of the product that engages in the goal seeking activities representationalism is supposed to explain. Mayr rejected historical accounts of genetic programs for just this reason:

“My definition of teleonomic has been labeled by Hull (1974) as a “historical definition.” Such a designation is rather misleading. Although the genetic program ... originated in the past, this history is *completely irrelevant* for the functional analysis of a given teleonomic process. For this it is entirely sufficient to know that a “program” exists which is causally responsible for the teleonomic nature of a goal directed process. Whether this program had originated through a lucky macromutation ... or through a slow process of gradual selection, or even through individual learning or conditioning as in open programs, it is quite immaterial for classification of a process as “teleonomic.””²⁷ (my emphasis)

It is worth noting Mayr's rejection of teleosemantics as a reminder that even the most diehard adaptationist (and Mayr certainly was that), need not think representational content is defined in terms of natural selection. It is obvious why biologists and philosophers of biology would gravitate to teleosemantics, but there are other theoretical options.

Teleosemantics has its defenders who have attempted to answer this worry,²⁸ but I suspect these defenses fail. Most emphasize that items with a particular history of selection tend to have certain causal features, but then it is these causal features, not the history of selection, that is doing the theoretical work. It is important to distinguish extensional adequacy from a definition that captures the causal significance of a category. Chemists could define helium as the product of a particular kind of fusion reaction in stars, supernovae explosions, or the big bang, or a product of radioactive decay of atoms that were formed in the aforementioned processes. Such a definition, if carefully tweaked would pick out all and only helium, but it would not aid chemists or astronomers in their explanatory goals. How helium came to exist is an interesting question but answering it does not tell one how to expect helium to interact—or usually not, as it turns out—with other things. A definition in terms of atomic number is favored because it does explanatory work, and it does explanatory work because it highlights the causally relevant features of helium.

Whether or not my suspicions of teleosemantics can be answered satisfactorily, the cogency of genetic intentionality does not rest on the cogency of teleosemantics. First, note that teleosemantics rendering representations explanatorily inert is a general problem with teleosemantics, not a problem specific to genes. An explanation that so and so missed his flight because he believed the plane to be departing from gate A2 when it was in fact H5, does not appear plausibly rendered as a claim about the history, evolutionary or otherwise, of how the subject's brain state came to be correlated with facts about airplane departures. If this problem can be solved for thought and language, it seems likely the same solution would apply to genes, and if not, then the

lesson is that teleosemantics is not the correct account of intentionality, not that genes do not have intentionality.

Some alternatives to teleosemantics in the domain of language and thought, like theories that invoke inferential roles or social norms, would not apply straightforwardly to genes. However, there are other options that look more promising. Jerry Fodor has defended a view he calls asymmetric dependence theory.²⁹ On Fodor's view, the word 'cow' and the concept COW represents cows because there is a lawlike connection between the presence of cows and tokenings of 'cow' and COW. And, any tendency for the word or concept to be tokened in the absence of cows asymmetrically depends on the tendency for it to be tokened in the presence of cows. That is, if cows did not tend to cause tokening of 'cow', then distant horses, cow facades, and drug induced cow hallucinations would not either, but not the other way around.

It is less than straightforward to apply Fodor's idea to genes, primarily because the view is developed to apply, in the first instance to representations with a world to word direction of fit³⁰ like a declarative statement, but genes are typically conceived to act more like imperatives, with a word to world direction of fit. But, Fodor's account is meant to be general, and I suspect he would account for imperatives by simply reversing the direction of the lawlike regularities. That is, not only do cows tend to cause tokenings of 'cow', but 'cow' tends to cause instances of cow-related activities, and any activities involving distant horses caused by tokenings of 'cow' asymmetrically depend on the lawlike connection between 'cow' and cows. Applied to genes, this view would say that there is a lawlike regularity that genes coding for trait *X* tend to correlate with the presence of trait *X*, and any tendency for other traits to occur as a result of the gene asymmetrically depend on its law-like connection with trait *X*. This is far from a full theory of genetic intentionality. In particular the nature of the lawlike relations and the dependence relation need spelling out, but my point is not

that Fodor is correct, only that he is not obviously wrong and the view is *prima facie* compatible with genetic intentionality.

The view I favor, but will not defend in depth here, agrees with teleosemantics that intentionality is a matter of having the function of carrying information about or mapping onto a particular kind of thing in the world, but rejects the claim that functions are defined historically. According to causal role theories of functions, an item's function is its contribution to the dispositions or capacities of a larger system.³¹ The heart has the function of pumping blood insofar as its capacity to pump blood in part explains the capacity of the circulatory system as a whole to transport materials through the body in a *functional analysis* of that complex capacity. A functional analysis consists in a specification of how simpler dispositions are organized so that together they give rise to a more complex disposition. On this view, representations are items whose disposition to carry information about or map onto particular things partly explains the capacities and dispositions of the system in which they occur to behave in particular ways. Given that the explanatory goal is how a system comes to behave in a way that, as Fodor puts it, "reliably comports with its utilities," this view strikes me as especially promising. Tendencies of particular components to carry information about or map onto particular bits of the world in an organized way so that the system as a whole is disposed to stand in particular relations to the world fits perfectly with the explanatory role representations are supposed to play in Mayr's and Fodor's arguments for positing them.

Most philosophers have rejected this view because it is widely agreed that this view cannot capture the notion of misrepresentation because the causal role notion of function cannot capture the possibility that an item cannot perform its function. A disposition an item does not have cannot be its contribution to the workings of a larger system, so it appears that this view cannot allow for an item that has the function of φ -ing but is incapable of doing so. I argue at length in a companion

paper (see Dissolving the Dysfunction Dilemma) that this objection is misguided, but defending my account of dysfunction is beyond the scope of this paper. However, if I am right, then we have available a view of intentionality that captures the explanatory role of representations and applies naturally to genes, animal signals, human language, conceptual cognition, natural language, and digital computers. Whether it is right or not, the theoretical availability of this view reinforces that teleosemantics is not the only option for explicating genetic intentionality.

The literature on genetic intentionality has tended to focus on analogies between language and genes emphasized by molecular biologists, so has taken the theoretical question to be what explanatory role these analogies could play. If our reason for treating genes as representations is to explain end-directed processes, then the theoretical burden is not to show that genetic representation is explanatorily useful but to develop a theory of intentionality that captures the explanatory role for which representations have been posited in the first place. Explaining the goal directedness of living systems is a more powerful motivation for taking genetic representation seriously in part because it makes genetic intentionality plausible, even in the absence of a specific theory of intentionality. This expansion of scope for theory development should not prove too difficult given that the explanatory puzzle is the same one representational theories of mind are already designed to solve.

There is a second problem of explanatory inadequacy that must be addressed. Many researchers suspect that representational explanations give rise to an illusion of explanatory completeness, thereby removing the impetus to address important questions. Robert Lickliter and Thomas Berry approvingly note that several authors have “pointed out that this willingness to assign information to development to a genetic “program” or “blueprint” can and often does lead to the belief that the process of development is thereby somehow explained or understood, eliminating the need for any further investigation or research.”³²

Strictly speaking, this is not an objection to the notion that genes carry intentionality but an objection to the way researchers tend to behave under that assumption. But, it is worth noting that this problem can be mitigated if genetic intentionality is justified by the need to explain the end-directedness of biological processes. If genetic intentionality is inferred from mechanistic similarities between genes and digital computers, the inference carries the assumption that there is already a background theory of implementation in place when semantic concepts like program or blueprint are invoked. Biologists have largely presumed that those questions have been answered by computer science and information theory. However, with genetic intentionality directly justified by the explanatory role of semantic properties per se, we are left with the question of how the relevant representational-cum-computational processes are implemented. The Mayr/Fodor argument for representationalism does not carry with it the presumption that the implementational details in the case of genes will be similar in any particular respects to other familiar representational systems.

David Marr's influential distinctions among computational, algorithmic, and implementational problems are salient here. Having isolated the computational problem, say developing a limb, there remains the task of actually spelling out the algorithm that solves this computational problem. It is a non-trivial task that is not satisfied by simply noting that there is a program, though it may be a problem that can be black-boxed for the purposes of some explanatory goals. And, having described an algorithm, there remains the implementational problem of spelling out how this algorithm is realized in a physical system. Marr's distinctions have been influential in cognitive science, and Lickliter and Berry's objection highlights the need for biologists to be aware of it, rather than any theoretical problem with computational/representational explanations precluding the elucidation of mechanisms.

This division also corresponds roughly to theoretical distinctions already recognized in the practice of developmental biology. Consider a standard explanatory model of pattern formation

during development, for example the development of zebra stripes or leopard spots. On Marr's framework, this represents a computational problem, an end that cries out for an algorithmic explanation. Alan Turing developed an influential mathematical model demonstrating that biological patterns, and more generally deviations from symmetry, can be explained by positing a short-range activator and a long-range inhibitor diffusing at a given rate.³³ Turing did not link his model to his work on computation, though others have done so.³⁴ Thus, it may be that Turing's model can be viewed as an algorithm, but in any case the model leaves open whether and how the components are realized in a real biological system. As Ingo Brigant has noted, these models provided only "how-possibly" explanations for many decades, but there has recently been experimental work on the implementation of such systems in real organisms.³⁵ This example shows that something akin to Marr's levels of explanation are already embodied in the practices of developmental biologists. A general process or algorithm that would explain how the system achieves a given end is suggested, followed by a search for concrete physical processes in real organisms that instantiate the process.

Another way of resisting the tendency to take explanations invoking representations as a complete story is to recognize that citing representations to explain particular end-directed processes leaves open important theoretical questions about the representational system itself. Fodor's argument is usually presented as an argument for a "language of thought." I will return to this notion in Section 5, but we can provisionally think of Mayr's argument as a parallel case for a "language of inheritance." If the idea of the genome as a linguistic entity is to do any theoretical work, then the onus is on biologists to address the different aspects of linguistic theory, including the system's orthography, syntax, semantics, and pragmatics. In addition to providing details about algorithms and their implementation, there remains the task of explicating the physical realization of the symbolic elements (orthography), the rules governing relations between elements (syntax), how its elements map onto the environment in which it is embedded (semantics), and how the system

behaves in a given context (pragmatics). I will argue in the next two sections that recognition of these theoretical burdens is essential for addressing the other two major pitfalls facing the view that genes are representations.

4. Problem 2: Context Sensitivity

One of the primary motivations for resisting genetic intentionality has been the sense that thinking of genes representationally encourages a simplistic picture of the relationship between genes and traits. Susan Oyama has claimed that eliminating informational (that is, representational) conceptions of genes is the “stake-in-the-heart move” that will finally kill the error of genetic determinism in the life sciences.³⁶ Like the last objection considered in Section 3, this is not, strictly speaking, an objection to the idea of genetic intentionality but a diagnosis of the psychological source of a particular kind of theoretical mistake. Paul Griffiths leverages this diagnosis into an objection to genetic intentionality when he claims that “intentional information is intrinsically context insensitive and thus intrinsically unsuited to express the causal link between genes and complex phenotypes.”³⁷

Whether representational conceptions of genes have led researchers to more naturally make simplistic assumptions about genetic causation is an empirical question—and, those who have alleged that they do, in my view, have not made a convincing empirical case for representational notions playing a causal role in genetic determinist tendencies. But, for the sake of argument, assume that there is a link. What can we conclude? It may be that representational notions of genes have been misleading because genes are not actually representational. Or, it may be that these inferential errors occur because biologists by and large have an overly simplistic picture of language and other representational systems. In this case, the best way to critique problematic inferences may be to correct mistaken assumptions about representational systems rather than to reject representational

conceptions of genes. By taking the latter route, critics re-enforce the very inferential mistakes they seek to expose by implicitly endorsing the simplistic picture of representation that is their source.

Stephen J. Gould dismisses the idea that genes have representational content out of hand on the grounds that the causal connection between genes and traits is extraordinarily complex.³⁸ Biologists are rightly fascinated by the staggering complexity in life but have underestimated the complexity of intentional systems. When one uses the word 'proton' it refers to protons, but only via a complex web which includes not only one's own representations, but the representations of a complex network of other humans, as well as lab equipment, documents, printing presses, funding agencies, research practices, and the list goes on. The causal network linking my use of 'proton' to protons is at least as complex as the causal network linking genes to traits, and probably includes them. Gould's point about complexity would be better served by recognition of the complexity of representational systems than by dismissing genetic intentionality. Similarly, Oyama claims that representational conceptions encourage a kind of dualism between genes and the rest of the organism, making them the Cartesian mind to the biological body.³⁹ But, if biologists are tempted to a kind of dualism by representation-talk, the problem is the assumption that representations require dualism, not the assumption that genes are representational.

Appreciating the possibility that it is an overly simplistic picture of representation that leads to, or at least accompanies, overly simplistic assumptions about genetic causation, rather than the idea of genetic intentionality per se, removes much of the impetus to find a Griffiths-style explanation for what it is about representational conceptions of genes that would make them misleading. Still, it is worth considering Griffiths's claim that intentional information is intrinsically context insensitive. It appears to be implausible on its face, since there are clearly many cases of context sensitivity in representational systems. Ambiguous terms like 'bank' and context sensitive

terms like ‘here’, ‘now’, and ‘I’ are all familiar cases of context sensitivity in language. However, the mere existence of context sensitivity in language may not be enough to answer Griffiths’s challenge.

Griffiths makes it clear that the kind of context insensitivity he has in mind is continuity of reference across contexts. The existence of cases like ‘here’ and ‘now’ show that representations are not intrinsically context insensitive in the strong sense that reference cannot vary across contexts, but Griffiths and others who suspect representation cannot capture the context sensitivity of the link between genes and traits emphasize that this context sensitivity is pervasive and complex. Simply noting that we must fill in a location, time, and speaker to determine the meaning of ‘I am here now’ does not show that representational conceptions can capture the complexity and pervasiveness of the role of context in linking genes to traits. Griffiths is surely aware that context sensitive expressions are part of many representational systems, but I suspect that he envisions these as a specific phenomenon that includes few parameters and must occur against the backdrop of a system that is largely context insensitive. In fairness to Griffiths, biologists who employ representational conceptions of genes likely assume the same.

However, cases like ‘bank’, ‘I’, ‘here’, and ‘now’ are not atypical. In fact, there is universal consensus among linguists and philosophers of language that natural language is wildly context sensitive. The Stanford Encyclopedia of Philosophy article “Indexicals”⁴⁰ provides a convenient list of the multifarious kind of expressions that are likely context sensitive in the same sense as terms like ‘now’, ‘here’, and ‘I’. I list below some examples.

- *Tense terms*: is, was, were...
- *Modals*: necessary, possible, must, might, could, may, can, able...
- *Gradable adjectives/adverbs*: tall, old, rich, fast, smart, fairly, very, good, bad...
- *Adjectives/Nouns that take complements*: neighbor, ready, late, relevant, local, eligible, enemy...
- *Location terms*: left, behind, near, under, around...

- *Quantifiers*: some, all, most, few, many...
- *Deontic Terms*: ought, should...
- *Propositional Attitude Verbs*: believes, desires, hopes, knows, wants...
- *Conditionals*: If *X* then *Y*, Given *X* ...
- *Vague expressions*: red, bald, pile, island...

It is worth noting that this last category of vague expressions arguably contains many more things than one might initially suppose. Imagine a chair, a stool, and table, each with four legs. Consider how low and wide and low a stool would need to be before we would say that it is actually a table. How high must the back of a chair be to count as a chair, rather than a stool. Perhaps functional considerations would help, but it is possible to rest one's drink on a stool, to sit on a table, and to have a drink at a bar while sitting in a chair. Considerations like this suggest that the boundaries between very many common categories may be vague.

Some authors have claimed that all expressions are context sensitive.⁴¹ According to John Searle, "in general the meaning of a sentence only has application (it only, for example, determines a set of truth conditions) against a background of assumptions and practices that are not representable as a part of meaning."⁴² If this is right, then natural language at least, and possibly representation more generally, is intrinsically context *sensitive*, contrary to Griffiths claims.

Not all linguists and philosophers of language agree that all the expressions listed above have a context sensitive semantics, much less that all expressions do. However, this controversy obscures an underlying agreement. Those who deny pervasive context sensitivity at the level of semantics do not deny that context sensitivity is present in these cases, only that it should be included in the semantics. Consider Herman Cappelen and Ernest Lepore's defense of the view they label "semantic minimalism." Cappelen and Lepore argue that context of utterance has very limited effect on an

utterance's semantic content, but they are only able to make that view plausible by also defending a view they call "speech act pluralism." Here is their summary of speech act pluralism.

"No one thing is said (or asserted, or claimed, or . . .) by any utterance: rather, indefinitely many propositions are said, asserted, claimed, stated. What is said (asserted, claimed, etc.) depends on a wide range of facts other than the proposition semantically expressed. It depends on a potentially indefinite number of features of the context of utterance and of the context of those who report on (or think about) what was said by the utterance."⁴³

Capellen and Lepore agree that what is expressed by any given utterance is in general wildly context sensitive; they simply deny that this is a feature of the semantics. The disagreements among linguists and philosophers of language concerns where to draw the line between semantics and pragmatics, not about whether what is expressed by any given instance of language usage is context sensitive. In light of this consider Griffiths diagnosis of the role of representational conceptions of genes in encouraging genetic determinism.

"Allowing genes to retain their imperative link to a particular phenotype across changes in causal context creates a background assumption that if the gene were expressed, it would produce the phenotype about which it contains information. The intentional representation of the gene also makes it natural to think that environments in which the gene does not "express" its meaning are qualitatively different from those in which it does; such environments are somehow abnormal or pathological because they create a *mismatch* between gene and phenotype. In all these related ways, the intentional representation of the gene supports the idea that genes have constant effect across context, and hence the idea that genetic and environmental factors interact additively."⁴⁴ (Griffiths emphasis)

If these are the inferential patterns that lead researchers to genetic determinist inferences, then it is clear that misconceptions about representation are at work. It is uncontroversial that natural language utterances do not express anything truth evaluable independently of “a potentially indefinite number of features of the context of utterance.” Many have attempted to incorporate this into semantic theory, while others argue that these features are to be explained at the level of pragmatics.

It is difficult to pin down exactly what is at issue in debates about the border between semantics and pragmatics—this is one reason they have been ongoing—but much of what is at issue concerns which aspects of meaning are compositional. One of the central explanatory concerns in linguistics, and one of the features that allow semantic representation to explain goal-directed activities, is that the meanings of complex expressions are composed systematically out of the meanings of their components. This semantic compositionality is mirrored by syntactic compositionality, which is in turn mirrored by the causal structure of a computing device.

I noted at the outset that the Mayr/Fodor argument does not directly support the idea that it is genes in particular that carry intentionality, but insofar as the explanatory strategy relies on a language-like compositional structure at the level of syntax, semantics, and form, we have a reason to think of the discrete, plausibly compositional, hereditary factors as the ones with semantic values and the rest as part of pragmatic context. This may not isolate only genes in the narrow sense—I see no reason methylation patterns, for example, might not be discrete in the right way—but, I suspect it does more or less vindicate the standard division of genes and environment that some critics have sought to undermine. And, it coheres especially well with John Maynard-Smith and Eörs Szathmáry’s claim that both genes and language allow for what he calls “unlimited heredity,” while other modes of

inheritance do not.⁴⁵ However, if the discrete compositional features of genes justifies thinking of them as carrying semantics while other features are part of pragmatic context, the arguments of this section should allay worries that this amounts to relegating those other causal factors to secondary status. Linguists and philosophers of language agree that if we want to explain how language is actually used to do anything, the bulk of the explanatory weight is carried by context.

The upshot of this section is that in the most uncontroversially representational system, natural language, context sensitivity is pervasive and wildly complex. Therefore, there are no grounds for the claim that representation is intrinsically context insensitive in any interesting sense. A more realistic picture of the way language actually works would likely mitigate any tendency for representational conceptions of genes to lead to genetic determinism. This may be true even if it turns out that mistaken assumptions about representation are a symptom rather than a cause of genetic determinist inferences.

It is also worth noting that in the realm of mental representation, too, there has been growing awareness of the need to consider context. The movement to think of cognition as embodied is a case in point. Though many claims have been associated with the call to recognize that cognition is embodied,⁴⁶ two in particular are relevant here. First, cognitive scientists have increasingly recognized that we cognitively offload processing onto the environment. A shopping list is a particularly mundane example. In one famous study it was shown that expert Tetris players, but not novices, offloaded the cognitive process of mentally rotating blocks by rapidly pressing the rotate button, thereby allowing for quick perceptual recognition of optimum game moves.⁴⁷ Second, somewhat more controversially, some have argued that mental representations extend beyond the brain, and possibly beyond the body. That is, mental representations may actually include environmental components. I

suspect defenses of developmental systems theory, which emphasizes the role of environmental variables in development, would be better served by aligning itself with this extended conception of representation, rather than attempting to undermine representational conceptions of genes.

5. Problem 3: Implementational Details

Critics sometimes point to specific genetic mechanisms to argue that genes are not representational. In some cases, these mechanisms are meant to simply point to cases of complexity or context sensitivity, points that I addressed in the previous section. In other cases, the argument is that the initial characterization of the genetic code in the specific sense of the mapping of nucleotide triplets to amino acids does not extend naturally to more complex traits. For example, Sarkar cites multiple splicing as a factor blocking the application of some informational notions that were helpful in sorting out the genetics of *E. Coli* to the case of prokaryotic cells.⁴⁸ In still other cases, the point seems to be to simply point to disanalogies between genes and language. Sarkar notes that many regions of DNA do not code for proteins while languages do not contain masses of meaningless text. These strategies are not always independent. For example, Sarkar points to multiple splicing as an example of the context dependence of which proteins are produced as a result of a given segment of DNA.

Godfrey-Smith has noted that Sarkar's point about non-coding regions does not undermine the idea that genes are representational because representational systems can vary, and though natural languages do not have large segments of meaningless text, it does not follow that this is essential for being a representational system.⁴⁹ This type of response can be generalized. Given that the initial motivation for many representational concepts in genetics arising from mechanistic analogies with systems like Morse Code, it is important to recognize points where the analogies break down. But, given the Mayr/Fodor argument for genetic intentionality, mechanistic details

largely fall away as irrelevant to assessing the cogency of representational characterizations of genes, because the argument presumes nothing about implementational details. We should thus regard with suspicion any argument that moves from a claim about the details of molecular biology to the claim that genes do not have semantic content.

This is not to say that implementational details are completely irrelevant to the cogency of representational and computational characterizations of genes. A computational theory cannot be correctly applied to a system that cannot implement it. But, the arguments here support the usage of representational concepts to explain goal directedness, so we would expect representational characterizations to pull their explanatory weight in higher-level fields concerned to explain how systems achieve certain goals. Taking seriously the parallels with other domains in which this explanatory strategy applies suggests that genes can implement computations but that we should expect details of molecular biology and claims about genes representing phenotypic traits to be, for all practical purposes, autonomous.

First, note that though we need not assume parallel implementations for genetic and cognitive representations, there are promising theoretical avenues for a unified treatment. Roger Sansom has argued that gene regulatory networks can be captured by connectionist networks, which are already influential tools in cognitive science.⁵⁰ Connectionist networks can implement classical language-like architectures, so as Murat Aydede has argued, it is a theoretically viable option to believe in a Fodor-style language of thought implemented in a connectionist network.⁵¹ The same point should hold for the idea of a “language of inheritance.”

Second, connecting implementational details to high level representations like instructions for developing phenotypic traits would likely include multiple levels of representational description. Consider an easy case, a standard home computer. A standard user does things like click icons and read on screen messages, and there is a very high level representational description of these sorts of

interactions. But, this system is implemented by a programming language, often a high-level language like Python. But, Python is itself implemented in a lower level programming language, usually C. C is in turn implemented in an assembly language, which is in turn implemented in machine code. The semantics at each level looks very different. While the standard user refers to things like folders, icons, and text, primitive terms in high level languages may refer to abstract mathematical functions, and machine code expressions refer to things like register locations. Note that the semantics of higher level representations need not be straightforwardly related to the semantics of the representations they are implemented in.

Here the top down Mayr/Fodor argument for genetic intentionality meets up with the bottom up mechanistic analogies that originally motivated many biologists to think of genes as computational/representational. Taking both motivations seriously, we should expect genetic semantics to look a lot more like machine code than like belief-desire psychology. If so, Godfrey-smith, Sarkar, and other critics are correct that the kinds of localized sequences typically envisioned in the search for a “gene for trait *X*” only semantically represent particular proteins, and that this does not extend to phenotypic traits. Genetic semantics at a molecular level would refer to proteins much like machine code refers to particular bits of hardware. This image of genes coheres well with biologists’ usage of representational and informational concepts to link developmental and transmission genetics. Transmitting traits across generations would be a lot like sending an image as a bitmap. Taking the analogy between genes and machine code seriously should quell rather than encourage any tendency to slip into inferences that assume a simplistic “one gene, one trait” model. Just as an image is a global feature of a bitmap, traits would only be represented by the entirety of a genetic network.

Finally, it can be useful to invoke higher level representations that are only implicit in, or even merely abstractions from, the total representational system or its implementation. For example,

we typically treat beliefs as if they are closed under logical entailment, at least in simple cases. If I believe that it is Friday, July 13th, then I also believe that it is not Thursday, that it is not the 27th, that it is Friday or Saturday, that July 13th falls on a Friday, and so on. In an important sense, we all have an infinite number of beliefs, but even those like Fodor who believe in a direct implementation of a language of thought in the brain that closely mirrors belief-desire psychology must agree that the vast majority are not explicitly encoded in our brains.⁵² Fodor has claimed that these implicit representations will not do any explanatory work, but others disagree.

Robert Cummins has noted that representational content can be implicit in various features of the representation's structure, and provided several useful examples:⁵³

- 1) That a search routine in a word processor is checking for a match between the second character of the input and the current character being read means that the character read previously matched the first character in the input. Cummins calls this representation implicit in the state of control.
- 2) The standard algorithm for multiplication using Arabic numerals relies on the equivalence between shifting a column to the left and multiplying by ten. This would not work with Roman numerals. Cummins calls this representation implicit in the form of representation.
- 3) If two plane figures are drawn on two transparencies, one can test for congruence between the figures by aligning and rotating the transparencies, because the medium itself encodes the fact that relative spatial locations of parts of the figures are fixed. Cummins calls this representation implicit in the medium of representation.
- 4) "I give you instructions for getting to my house ... Perhaps I even include things like "Make a left down the alley with the blue Chevy van parked in it," because I know you will be coming after 5 o'clock and I know that the van is always parked there after that time. Now, if you (or anything else) executes this program, you will get to my house. In the process you never create a

representation of the form “Cummins lives at location L”; yet, given the terrain, a system for executing this program does “know where Cummins lives.”⁵⁴ Cummins calls this representation implicit in the domain.

This final kind of case is especially interesting because it shows that higher level representational characterizations can depend on the interaction between another level of representation and its context. The disposition to execute the instruction “Make a left down the alley with the blue Chevy van parked in it,” plus the van’s tendency to be there after five, plus its being after five, all ground* the higher level representational claim that the system executing the program knows where Cummins lives. In the case of genes, it may be possible for a context sensitive set of genetic instructions for a set of traits, together with the relevant contextual features, to realize a higher-level representation of how all or part of an organism is put together. Perhaps developing this line of thought could vindicate the idea that genes are a blueprint, map, or recipe for building an organism despite much of the relevant information being implicit in the environmental context.

Daniel Dennett has argued that belief-desire psychology tracks noisy but real patterns in lower level mechanisms, and that these patterns can be more useful for our explanatory purposes in many cases than details about the underlying system.⁵⁵ His most quoted example involves one programmer critiquing another’s chess program by noting “it thinks it needs to get its queen out early” despite there being no line of code in the program corresponding to the instruction “get the queen out early.”⁵⁶ Whether or not Dennett is right about belief-desire psychology, we must still be aware of the possibility that very high level representational descriptions may, strictly speaking, not be implemented in lower level representation so much as abstracted from them. He has emphasized

* I use the term ‘ground’ here in the vernacular sense that has inspired the current literature on metaphysical grounding, rather than in any precise technical sense arising from that literature.

that on his picture, multiple incommensurable representational schemes may be equally fruitfully applied to a given case. I have been moving through theoretical justifications for increasing levels of autonomy between molecular biology and higher-level claims about genes representing or coding for traits. If some claims about genetic representation of traits works like Dennett thinks belief-desire psychology does, then molecular details would provide close to no constraint at all.

6. Conclusion

I do not take the foregoing considerations to have established that genes have intentionality. Rather, I have argued that Ernst Mayr's argument that a computational and representational conception of genes is needed to explain the end-directedness of biological processes like development and behavior makes the idea much more plausible than an argument from mechanistic analogies between molecular processes and digital computation. Mayr's argument is, in essence, the same one that has justified representational and computational theories of mind, which have been a pillar of the background theory of cognitive science for over half a century. With this parallel in view, there are many lessons to be taken from cognitive science and philosophy of mind for developing the idea that genes carry intentionality. Here I have focused in particular on answering some of the major challenges facing representational and computational conceptions of genes.

It has been argued that genetic intentionality is explanatorily inert. This criticism is not a special problem for genes; it has long been a sticking point for critics of computational and representational theories of mind.⁵⁷ The same theoretical options are available for answering the challenge in the case of genes. Due to the central place of teleosemantics in the debate about genetic intentionality, I have focused on the problem as it relates to that particular view and suggested alternative theoretical options. Some have also alleged that representational and computational explanations provide a shortcut for a real mechanistic explanation and deter valuable research on important questions. In one sense, this is exactly the point. Sometimes it is useful to abstract from

the details. But, the worry is well-founded, and I have argued that biologists that employ computational and representational notions should keep in view important distinctions between different levels of explanation in representational systems. Both Marr's tripartite distinction between computational, algorithmic, and implementational levels, and linguists' division of representational systems into phonology/orthography, syntax, semantics, and pragmatics, are important for avoiding the mistake of conflating a computational account or generalization and an account of its implementation in a concrete system.

Keeping in view that semantics and pragmatics together are required for making sense of the meaning of any actual utterance or inscription in natural language also undermines the objection that representational and computational conceptions of genes obscure the context sensitivity of their phenotypic effects. On the contrary, if natural language is any indication of a general pattern—it strikes me as extremely likely that it is—we can expect context sensitivity in most representational systems to be pervasive and wildly complex. If representational conceptions of genes have been associated a tendency to make inferences that assume a simple relation between genes and traits, this should be mitigated by an appreciation of the complexity of the relationship between even ordinary language and the world it represents. Biology gained much from the methods of historical linguistics when they began tracing species lineages, so it would not be unprecedented if linguistics once again contributed to biological methodology for handling context sensitivity.

Finally, some have claimed that particular molecular details somehow tell against genes having semantic content. In many cases this is simply a way of making arguments about context sensitivity, complexity, or explanatory inertness. But, it is not always clear that this is the argumentative strategy at work, so I have argued more generally that molecular details and representational claims about genes are largely autonomous. In addition to distinctions between implementation and representation already mentioned, there are also multiple representational levels

separating molecular details from claims about genes representing traits. There is a hierarchy of programming languages mediating the relationship between the lowest level semantically evaluable computational processes in a home computer and the familiar user interface with which most people mostly interact. Similarly, the most plausible picture of genetic representation would not have protein coding sequences directly representing complex traits. Rather, these sequences would act like a machine code that implements higher level representations that are distributed across the genome. Since the semantics of higher level representations may be an implicit, distributed, global, contextualized, and/or abstracted feature of the representational level in which it is implemented, we can expect a great deal of autonomy between the computational/representational characterizations in molecular biology and those in fields like developmental and evolutionary biology.

I have not discussed here the more specific theoretical work genetic intentionality can do. Many of the details of have yet to be developed, and ultimately the idea of genetic intentionality will be tested by the theoretical and empirical work it enables. Already projects like Maynard-Smith and Szathmary's work on major evolutionary transitions⁵⁸ and David Sloan-Wilson's work applying genetic heat mapping techniques to religious texts⁵⁹ provide some concrete evidence of the theoretical fruitfulness of the idea, beyond the abstract Mayr/Fodor argument. Representational theories have been extremely fruitful for studying cognition, and cognitive science emerged as a unified field only with the adoption of computational theories of mind. If the explanatory task facing developmental and behavioral biology is in essence the same one, representational and computational conceptions of genes are a good theoretical bet. As noted at the outset, representational theories of mind and genes do not stand or fall together. However, given the parallels in motivations for and problems facing computational/representational theories of mind and computational/representational conceptions of genes, I suspect that genetic intentionality will fit naturally into any successful theory of intentionality. The trick now is to develop one.

Notes

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Chapter 3: Disentangling and Integrating Mayr and Tinbergen

1. Introduction

Research on animal behavior is typically organized according to a combination of two influential frameworks: Ernst Mayr's distinction between proximate and ultimate causes¹, and Niko Tinbergen's "four questions,"²— concerning mechanisms, development, survival value, and evolution. The two frameworks are generally taken to be unified, with Mayr's proximate-ultimate distinction marking one of two axes dividing Tinbergen's four questions, as depicted in the table below.³ The other axis divides the non-historical and the historical. My aim here is to argue that this picture of the relationship between Mayr's and Tinbergen's frameworks is importantly misleading. Most significantly, not all explanations of survival value and evolution count as ultimate in Mayr's sense, only those which take the form of a narrative, population level explanation that invokes natural selection. And, the framework depicted in the figure leaves out a third category of Mayr's framework, which he calls "the role of chance" which is neither proximate nor ultimate.

Figure 3.

	Non-Historical	Historical
Proximate	Mechanisms (Causation)	Development (Ontogeny)
Ultimate	Survival Value (Function)	Evolution (Phylogeny)

My motivations are threefold: 1) Mayr's and Tinbergen's frameworks have been extremely influential, and form part of the standard conceptual repertoire of animal behavior researchers, and so it is important from a purely historical perspective to get the two frameworks and their relation to one another right. 2) Both frameworks represent sophisticated efforts by practicing biologists to address philosophical questions about the nature of biological explanation. Tinbergen's work has received little direct attention by philosophers, despite its influence in biology, so this essay will serve to begin rectifying this lack of attention. Though Mayr's work, on the other hand, has been much discussed by philosophers of biology, in my view much of the philosophical engagement with Mayr's work misrepresents his position. But, here I will focus on providing a positive account of Mayr's views rather than detailed critiques of extant interpretations. 3) Recent methodological controversies in biology (and to a lesser extent, psychology) about the cogency and import of integrative projects, like evolutionary developmental biology and evolutionary psychology, largely concern the boundaries and relationship between proximate and ultimate causes. Variation in conceptions of Mayr's views and their relationship to Tinbergen's have played a key role in these debates, so the historical and philosophical project of characterizing them more carefully has important ramifications for current methodological disputes.

2. Integration vs. Autonomy

Mayr introduced the proximate-ultimate distinction as part of a philosophical defense of the autonomy of evolutionary biology from molecular biology.⁴ By 1961, when Mayr published "Cause and Effect in Biology," in which the distinction is introduced, molecular biology was quickly monopolizing funding, academic positions, prestige, graduate students, and publications. In response to a growing sense that all biology would be reduced to molecular biology, and in turn reduced to chemistry, and finally physics, Mayr argued that this sort of reductionism confuses two kinds of causes, proximate and ultimate.

Mayr characterizes the proximate-ultimate distinction in four ways in his initial introduction of the terminology. First, proximate causes are the purview of “functional biology”—Mayr’s primary example is physiology—while ultimate causes are the purview of evolutionary biology. This disciplinary division is characterized by the questions each asks, so given that proximate and ultimate causes are cited in the answers to those questions, we have a second characterization of the distinction: proximate causes can be invoked to answer ‘how?’ questions while ultimate causes can be invoked to answer ‘why?’ questions. Third, Mayr claims that the distinction can be made using the notion of a genetic program: proximate causes concern the operation of the genetic program while ultimate causes involve the origin of the program. Finally, Mayr characterizes ultimate causes as those that “have a history and have been incorporated into the system through many thousands of generations of natural selection.”⁵ Each of these characterizations raise hard interpretive questions. Much of the rest of this essay will be concerned with explicating the proximate-ultimate distinction more carefully, but Mayr’s initial characterization provides the common ground in current controversies about integrative projects. Before offering my own interpretation of Mayr, I will summarize Tinbergen’s four questions and characterize the tension my interpretation will help to circumvent.

Tinbergen introduced his four questions in a paper entitled “On the Aims and Methods of Ethology” with the primary aim of honoring his friend and mentor, Konrad Lorenz.⁶ Tinbergen argues that Lorenz’s preeminent contribution was to show that it is possible to study behavior from a biological perspective, a perspective characterized by a particular set of questions. Following Julian Huxley,⁷ Tinbergen divides biological inquiry into three types of questions, concerning: 1) evolution, which encompasses both the historical progression and general mechanisms of evolutionary change, 2) survival value, and 3) “causation” (I will use the now more common term ‘mechanisms’), which includes both internal mechanisms and external triggers. To Huxley’s three questions, Tinbergen

adds a fourth: the question concerning development over an organism's lifetime. So, we can ask of a behavior: "How did it evolve?", "How does it contribute to survival?", "How is it mechanistically accomplished?", and "How does it develop over the lifetime of the organism?".

In addition to honoring Lorenz, Tinbergen uses the "Aims and Methods" paper to solidify the identity of the burgeoning field of Ethology. In particular, Tinbergen argues for a thorough integration of the biological study of animal behavior across disciplinary boundaries, including psychology, neurophysiology, and evolutionary biology. To this end, he notes that "in speaking of the "four problems of biology" we apply a classification which is pragmatic rather than logical" and that "a comprehensive, coherent science of ethology has to give equal attention to each of them and to their integration."⁸

Integrating Tinbergen's four questions requires more than answering each of the four individually. One can pick any four questions about any topic at random, and it would be clear that simply answering each would not constitute an integration of those questions. However, it is not immediately obvious what is required for a successful integration of the four questions. At the very least, integration would appear to require showing how the answers to the different questions dovetail with and constrain one another. There does not appear to be any interesting sense of 'integration' on which questions can be integrated if their answers are wholly independent. However, this very basic requirement leads immediately to a tension in the standard picture of the relationship between the proximate-ultimate distinction and the four questions.

Autonomy and integration pull in opposite directions. The more two explanations dovetail and constrain one another, the less autonomous they are. While Tinbergen emphasizes the pragmatic nature of his division between the four questions, Mayr emphasizes the distinctness and autonomy of 'how?' versus 'why?' questions. This alone is not a problem. Constraints that push in

opposite directions often provide a useful narrowing of theoretical options. However, it is no trivial task to draw the line between integrating proximate and ultimate questions and conflating them.

This tension is at the heart of heated controversies about the cogency and import of a number of integrative projects. The proximate-ultimate distinction is regularly invoked in critiques of integrative projects.⁹ For example, evolutionary psychology has been criticized on the grounds that it makes unwarranted inferences about proximate mechanisms based on speculations about ultimate causes. And, a number of researchers engaged in integrative projects have advocated rethinking or abandoning the proximate-ultimate distinction on the grounds that it is outmoded and a barrier to progress.¹⁰ Researchers in evolutionary developmental biology (evo-devo) in particular have suggested that Mayr's distinction carries with it the presumption that development is irrelevant to evolution, thereby precluding the integration of developmental and evolutionary explanations evo-devo seeks to provide. Given its status as standard textbook knowledge in the field, these suggestions are met with vigorous defenses of the distinction, along with accusations that the critics are making fundamental conceptual mistakes.¹¹ One defender of the proximate-ultimate distinction says of these evo-devo researchers "they have got their fundamental concepts wrong."¹²

To complicate matters further, the debate has revealed considerable variation among both critics and defenders of exactly what the proximate-ultimate distinction is.¹³ For example, there is a great deal of inconsistency about whether genetic drift can be an ultimate cause. This variation, coupled with the reasonable presumption that a distinction used to organize textbooks and introductory college coursework should be common ground, has been a recipe for partisans in the debate talking past one another.

For critics, this is only further evidence that we need to abandon the proximate-ultimate distinction.¹⁴ My sympathies lie with its defenders. With Mayr's proximate-ultimate distinction, Tinbergen's four questions, and the relationship between them properly interpreted, the proximate-

ultimate distinction is no barrier to integration of the four questions. Here, I will focus on the interpretive questions themselves and leave the lessons for current methodological controversies of the views I defend here for future work. But, my central interpretive claim will be that Mayr's and Tinbergen's frameworks fit together such that Mayr's case for autonomy and Tinbergen's conception of integration are not in conflict. I defend the view that both Mayr and Tinbergen conceive of integration in terms of functional analysis, as characterized by Robert Cummins,¹⁵ and that Mayr's proximate-ultimate distinction is compatible with this form of integration. Establishing this point will require arguing for the two sub-claims I made at the outset: 1) Mayr's proximate-ultimate distinction is not accurately described as one axis dividing Tinbergen's four questions, and equivalently, Tinbergen's four questions are not a simple refinement of Mayr's proximate-ultimate distinction. 2) Mayr does not view the proximate-ultimate distinction as exhaustive; he recognizes a third category which he calls "the role of chance."

3. Disentangling Mayr and Tinbergen

The assumption that Mayr's proximate-ultimate distinction parses Tinbergen's questions into two groups arises in part from Mayr's tendency to use 'evolutionary' and 'ultimate' as though they are synonymous. This and the fact that the usual reason biologists care about the survival value of a trait is to discern its role in the selective origin and maintenance of that trait make it natural to take ultimate causes to be those cited to answer Tinbergen's evolutionary and survival value questions. Mayr himself characterizes the proximate-ultimate distinction in terms of the kinds of questions proximate and ultimate causes are cited to answer. Construing Tinbergen's evolutionary and survival value questions as 'why?' questions and his developmental and mechanistic questions as 'how?' seems to seamlessly combine both Mayr's and Tinbergen's insights. I will call this view the standard view, since it has become part of the textbook presentation of the two views that most behavioral biologists encounter early in their training.

The standard view is not universal. Donald Dewsbury has explicitly rejected it, and those who do not think genetic drift is an ultimate cause are implicitly committed to rejecting it, since one can certainly answer uncontroversially evolutionary questions by citing drift—though I suspect many fail to notice this implicit commitment. But, it is the view most biologists, including most critics and defenders assume, despite the variations mentioned above in attempts to characterize exactly what distinguishes ‘how?’ from ‘why?’ questions.

Before addressing the details of either Tinbergen’s or Mayr’s frameworks, there are a few general considerations that tell against the standard view. First, note that the standard view is not obvious. In a review of Tinbergen’s presentation of the four questions in his less influential and earlier 1951 book, The Animal in its World, Sara Shettleworth divides Tinbergen’s questions differently: “the first three [mechanisms, development, and evolution] have to do with mechanism or, as Tinbergen puts it “How is it done?”; and the last [survival value] with function or “What is its use?” For Shettleworth, Tinbergen’s questions do not divide into sets of two; rather, survival value is most naturally categorized as a “why?” question and the other three as “how?” questions.

Alternatively, philosophers standardly (and mistakenly, I argue elsewhere) divide functional explanations into two types, historical and causal role explanations.¹⁶ The former concern a history of selection while the latter concern causal contributions to a disposition or capacity, and thus explain how a system works. Questions about survival value concern a trait’s causal contribution to an organism’s capacity to survive, so questions about survival value and thus explain how the system works. They could reasonably be categorized as proximate, if we take proximate causes to be those that concern how a system works. On this parsing, evolutionary questions are ultimate while the other three are proximate. The point is not that either of these alternative classifications is a correct representation of the relationship between the four questions and the proximate-ultimate distinction but that neither of them is *prima facie* less reasonable given Tinbergen’s and Mayr’s initial

characterizations of their distinctions.¹⁷ The standard picture is not simply an obvious corollary of Mayr's and Tinbergen's definitions as first presented.

Second, there is little to no textual evidence that Mayr or Tinbergen conceived of the four questions as a simple refinement of the proximate-ultimate distinction. One would expect that if the two frameworks were marking basically the same distinctions, Mayr and Tinbergen would have indicated this. However, neither ever cites the other in the relevant contexts, and it was not because they were not aware of one another's work. Mayr and Tinbergen were close personal friends, and a letter¹⁸ dated June 6th 1963 from Mayr to Tinbergen, Mayr thanks Tinbergen for having sent him a copy of "On the Aims and Methods of Ethology" and offers comments on the manuscript. Notably, Mayr says little about the four questions, instead focusing on critiquing Tinbergen's definitions of innateness and learning. Mayr then writes "I hope I sent you a reprint of my paper on "Cause and Effect in Biology," in which I have discussed some of the problems touched upon by you." This exchange confirms that the two were familiar with the other's work, and no doubt there was mutual influence. Other letters reveal that the two regularly traded manuscripts, recommended reading, and discussed issues in the field. They surely discussed these issues in person as well. But, all this makes the standard picture less plausible, not more. If Mayr took the proximate-ultimate distinction to map more or less cleanly onto Tinbergen's four questions, it would be odd for Mayr to say that Tinbergen's discussion merely "touched on" some of the same ideas. Given their familiarity with one another's work, it not citing one another would also be odd, if either saw their two frameworks as more or less alternative formulations of the same point.

Charity considerations also tell against the standard interpretation. Mayr and Tinbergen were well aware of one another's views, so Mayr was well aware of Tinbergen's insistence that the divisions between his questions is merely pragmatic. If Mayr saw the boundary between Tinbergen's questions as the same one he intended to mark with the proximate-ultimate distinction, it is very

likely he would have objected to Tinbergen's views about what separates the questions. A merely pragmatic boundary would not serve Mayr's theoretical goals. Similarly, Tinbergen was aware of Mayr's division of biology into two very distinct fields, with functional biology studying one kind of cause and evolutionary biology studying another, and he would likely have objected if he saw Mayr's boundary as the same one marked by his four questions, because it would undermine his own goal of bridging different sub-fields of biology. The very same considerations that have convinced many biologists engaged in integrative work that Mayr's distinction makes integration problematic would not likely have gone unnoticed by Mayr and Tinbergen themselves, but there is nothing in their published writings or correspondences that indicate any recognition of a tension.

The lack of conflict is also supported by Mayr's own claims about integration. At many points Mayr explicitly acknowledges that developmental and mechanistic considerations can contribute to evolutionary explanations. Here are a few:

- “Those developmental biologists who will work on this problem, together with the molecular biologists, will certainly make a far greater contribution to our understanding of evolution than those who present to the world a completely erroneous picture of the current beliefs of the Darwinians.”¹⁹
- “changes occurring during development are responsible for the divergence of different evolutionary lineages”²⁰
- “These findings [from evo-devo!] shed considerable light not only on previously completely puzzling developmental processes, but also on the causation of fundamental events (branching points) in phylogeny.”²¹

If Mayr took any cause invoked in an explanation of evolution to be ultimate, then either Mayr is being inconsistent, or he changed his mind. Though Mayr certainly changes his mind about details and is more careful in later work to acknowledge the role of mechanistic considerations in

evolutionary explanations, he remains consistent about the basic distinction between proximate and ultimate causes. Many of these acknowledgements occur in the same works, sometimes on the same pages, as his discussions of the proximate-ultimate distinction and critiques of other researchers for confusing the two.²² Mayr may have been confused, but it is more charitable to assume that he did not take every cause invoked in an explanation of evolutionary phenomena to be ‘ultimate’. Indeed, such a view would risk completely collapsing not only the proximate-ultimate distinction, but any distinction between biological causes and causes more generally, since evolutionary phenomena can be influenced by physical causes of all kinds—asteroid collisions, continental drift, and the earth’s rotation are some salient examples. Given Mayr’s goal of defending the autonomy of evolutionary biology by showing that it is concerned with different kinds of causes, this would be unacceptable. It is not only uncharitable to interpret Mayr such that his distinction collapses, but the examples above explicitly show that he did not take every cause relevant to explaining evolutionary phenomena to be ultimate causes. He has a narrower class of causes in mind.

Mayr also refined one component of his characterization in way that does not fit comfortably with the standard view. In his 1961 paper, Mayr emphasizes that functional biologists are concerned to answer proximate ‘how?’ questions while evolutionary biologists seek to answer ultimate ‘why?’ questions. This emphasis is still front and center in his 1982 book, The Growth of Biological Thought. At both points, Mayr is still actively engaged in the fight against reductionism. But, in his final book in 2004, Mayr notes that “This difference is not complete because in evolutionary biology one also occasionally asks “how” questions – for instance, how do species multiply?”²³ Mayr appears to be, slightly more indirectly than in the quotes above, explicitly recognizing that non-ultimate causes contribute to evolutionary explanations. Speciation is an evolutionary process, but understanding it requires exploring particular mechanisms that operate independently of selection. Perhaps Mayr has in mind things like geographical barriers, but in the

context of the above quoted remark about the relevance of development to branching points in phylogeny, he likely means more. This could be viewed as a concession or even abandonment of a deep distinction between proximate and ultimate, but I suspect it represents merely a relaxation of his emphasis on the differences between evolutionary biology and other areas of research owing to a largely successful campaign to defend the value and autonomy of evolutionary research. Mayr continues to emphasize the proximate-ultimate distinction in the same work, so again, the most charitable interpretation is that he simply saw no conflict between his distinction and non-ultimate causes contributing to evolutionary explanations.

Finally, the standard interpretation does not fit well with Mayr's emphasis on the historical character of ultimate explanations. I have noted that Mayr often uses 'ultimate' and 'evolutionary' as synonyms, but he also uses 'historical' as a synonym for both. This should give us pause about reading too much into Mayr's tendency to use other terms as proxies for 'ultimate' because, as I will explain in the next section, he clearly does not think 'ultimate' and 'historical' are literally synonymous in his proposed usage, so we cannot infer that he takes 'ultimate' and 'evolutionary' to be synonymous either. In addition, the distinction between historical and non-historical is the other axis, orthogonal to the proximate-ultimate distinction, dividing Tinbergen's four questions according to the standard picture. Evolution and development are historical while survival value and mechanisms are not. If the difference between proximate and ultimate causes consists in part in the latter but not the former being historical, then the standard picture cannot be accurate in treating the historical versus non-historical distinction as orthogonal to the proximate-ultimate distinction. When this picture is standardly paired with a historical characterization of the proximate-ultimate distinction, and it typically is, it is not clear that the standard picture is even internally coherent.

We can do better than the standard view, but I claim only that it is importantly misleading, not completely mistaken. On the view I defend, it will turn out that ultimate causes are linked to

questions about evolution and survival value in a way that they are not to questions about mechanism and development. But, the proximate-ultimate distinction is not simply a less specific version of the four questions.

4. Reduction vs. Analysis

Mayr draws a distinction between reduction and analysis. The proximate-ultimate distinction serves to show that reduction is impossible, but it is meant to leave open the possibility of analysis. I will argue that the relevant sense of analysis is captured by Robert Cummins's account of functional analysis, and that this same framework captures Tinbergen's conception of how to integrate the four questions. Sections 5 and 6 will address how exactly the proximate-ultimate distinction is supposed to block reduction but allow for analysis.

Mayr does not provide a detailed explanation of what he means by analysis, but he contrasts it with reduction in at least two ways. First, reduction seeks to completely explain a system's activities by breaking it down to its most basic components, while analysis, on the other hand, does not require breaking a system into its most basic components. An analysis may terminate at a non-fundamental level of organization, if no useful information about the activity of interest can be gained by breaking the system down further.²⁴ Second, Mayr claims that the primary problem with reduction is that it ignores the interaction between components of a system. We can thus infer that analysis does not ignore interactions. Both of these points occur (as far as I can tell) only in Mayr's final 2004 book, but they cohere well with his much earlier defenses of holism about the genotype and defense of organisms, as opposed to genes, as the units of selection, as early as his 1963 Animals Species and Evolution.²⁵

Tinbergen, too, endorsed a kind of analysis. In "Aims and Methods" he advocates for integrating disciplines studying different levels of organization through a process whereby "achievements of complex systems are, after a varying number of analytical steps, described in terms

of achievements of component systems.” This sort of analytical strategy is common in the sciences, and has been usefully and influentially described in a rigorous form by Robert Cummins.²⁶ Cummins calls this strategy *functional analysis* and defines function attributions within it as follows:

x functions as a φ in [a system] S (or: the function of x in S is to φ) relative to an analytical account A of S 's capacity to ψ just in case x is capable of φ -ing in S , and A appropriately and adequately accounts for S 's capacity to ψ by, in part, appealing to the capacity of x to φ in S .

For example, the circulatory system has the capacity to transport materials like oxygen, waste, and hormones to different parts of the body. We can decompose this capacity into several sub-capacities including pumping, directing flow, diffusing materials, and so on. The heart's capacity to pump blood contributes to the system's capacity to transport material. So, the function of the heart (x) in the circulatory system (S) is to pump blood (φ) because the heart is capable of pumping blood (φ -ing), and the standard physiological account (A) of how circulatory systems work adequately and appropriately accounts for the circulatory system's capacity to transport material (ψ), in part, by appealing to the heart's (x 's) capacity to pump blood (φ).

Note that Cummins's formulation is a general formula for, as Tinbergen puts it, describing the achievements of complex systems in terms of achievements of components. And, Cummins's account crucially relies on the possibility of iterating the process, accounting for Tinbergen's "series of analytical steps."

Note also that on Cummins's account, the interaction between components in an analysis is an essential part of the story. As Cummins puts it, a functional analysis shows how "the programmed manifestation of [the] analyzing dispositions amounts to a manifestation of the analyzed disposition," and here "programmed" means "organized in a way that can be specified in a program or flowchart."²⁷ I explicate Cummins's notion of organization in a companion paper, but

for present purposes, the key point is that analysis in Cummins's sense captures what Mayr and Tinbergen have in mind in their references to analysis, and this is useful for showing how Mayr's and Tinbergen's projects fit together.

Tinbergen's conception of how to integrate his four questions is most explicit in "Aims and Methods," where he writes the following:

"The fact that we tend to distinguish sharply between the study of causes and the study of effects is due to what one could call an accident of human perception. We happen to observe behavior more readily than survival, and that is why we start at what really is an arbitrary point in the flow of events. If we could agree to take survival as the starting point of our inquiry, our problem would just be that of causation; we would ask: "How does the animal — an unstable, 'improbable' system — manage to survive?" Both fields would fuse into one: the study of the causation of survival."²⁸

Combined with Tinbergen's claim that the difference between causation (what I have been calling mechanisms) and development is merely the time scale over which we view the system, the above remarks succinctly capture Tinbergen's vision of how three of the four questions are integrated. By thinking of behavior as one level in the middle of a hierarchy of functional analyses of the capacity of an organism to survive and reproduce, we can approach behavior as a whole to be analyzed through mechanistic and developmental questions or as a component of a larger causal process by investigating its contribution to the capacity to survive and reproduce.

Tinbergen's conception of integration through functional analysis can be straightforwardly extended to include evolutionary questions as well. As Tinbergen notes in "Aims and Methods," survival value is most often of interest to evolutionary biologists because of the role of survival and reproductive success in the process of natural selection. We can functionally analyze a population's

or lineage's dispositions to persist and change in particular ways through time by analyzing it into other dispositions, like the tendency for offspring to resemble their parents, the tendency of traits to vary, and the capacity for some individuals to survive and reproduce more successfully than others in the population. Tinbergen notes that we must make inferences about evolutionary history based on observations about current utility, so it would not be unreasonable to think he would accept the following generalization of his remarks on survival:

The fact that we tend to distinguish sharply between the study of causes and the study of effects is due to what one could call an accident of human perception. We happen to observe *survival* more readily than *evolution*, and that is why we start at what really is an arbitrary point in the flow of events. If we could agree to take *evolution* as the starting point of our inquiry, our problem would just be that of causation; we would ask: "How does the *lineage* — an unstable, 'improbable' system — manage to *change and persist*?" Both fields would fuse into one: the study of the causation of *evolution*. (Italics indicate my changes from Tinbergen's original, quoted above.)

We can view a behavior as a whole to be broken down or as a component of a larger causal system. If we "start with behavior," we can adopt a mechanistic, downward and inward-looking perspective, or a functional, upward and outward-looking perspective.²⁹ Mechanistic and developmental questions call for breaking a behavior down, while questions about evolution and survival value call for placing the behavior in a larger context. Here the standard picture gets something right. There is a reason to group survival value with evolution and development with mechanisms. Additionally, Tinbergen's claims that it is timescale which separates developmental and mechanistic questions emphasizes on the historical character of evolutionary explanations but not survival value. Thus, the two axes of the standard view thus correspond to ways of grouping Tinbergen's questions that are supported by the text. I deny only that the axis separating the upward

looking, functional questions from the downward looking, mechanistic questions, from the perspective that starts with behavior, maps cleanly onto Mayr's proximate-ultimate distinction.

In addition to survival value, evo-devo researchers have emphasized that to fully understand the process of evolution we must also explain the origin of the variation on which selection acts. As evidenced by the quotes in the previous section, Mayr agrees. A functional analysis of the tendencies of populations and lineages to change and persist must include not only the capacity of individuals to survive and reproduce, but also the tendencies of populations to vary and not vary in particular ways with respect to particular traits, which in turn is explained by the tendency of individual developmental systems to operate in the ways evo-devo researchers have elucidated.

Mayr and Tinbergen agree that biologists working in different areas, including those mostly concerned with proximate causes and those focused on elucidating ultimate causes, study a single, hierarchical causal system. The four questions are a guideline for shifting our perspective to highlight particular facets of the overall system. These perspectives are integrated into a total picture by functional analyses which show how the targets of explanation from one perspective are the tools of explanation from another.

However, the fact that developmental and other mechanistic factors can contribute to our understanding of evolution through analysis does not imply that those factors count as ultimate causes. If contributing to our understanding of evolution through analysis were sufficient to be an ultimate cause all biological research, and perhaps a lot of chemistry and physics, would all count as investigation of ultimate causes, rendering the distinction moot. Mayr isolates particular causes in the complex to block reduction. The remainder of the paper will focus on elucidating how Mayr's proximate-ultimate distinction serves that purpose.

5. Teleology and History

In “Cause and Effect in Biology” and later work, Mayr typically juxtaposes discussion of the proximate-ultimate distinction with two other topics: teleology and the role of chance in biology. Neither has received much attention in debates about the proximate-ultimate distinction, but the distinction is intimately bound up with them. It is no accident that Mayr treats the topics together.

In “Cause and Effect in Biology,” one of Mayr’s characterizations of the proximate-ultimate distinction says that proximate causes are invoked to answer ‘how?’ questions while ultimate causes are invoked to answer ‘why?’ questions. Mayr’s point is not that a linguistic distinction marks the biological one. We can use the word ‘how’ to ask about ultimate causes: “How did long necks contribute to the survival and reproduction of sauropod dinosaurs such that natural selection favored them?” We can also use ‘why’ to ask about proximate causes. A little context setting will help set up the correct reading. Consider the question “why does the moon move a little farther from the earth each year?” One might take this question to be asking for a reason, perhaps God’s reason, for moving the moon thusly, but the question would not be out of place in an astronomy class and simply asks for a causal explanation for the moon’s movement away from the earth. Now, consider the parallel question “why does the heart beat faster when there is caffeine in the system?” One could be seeking an answer in terms of selection, but the more natural reading is that it simply asks for the physiological mechanisms that explain the heart’s reaction to the presence of caffeine.

Rather, Mayr’s ‘how?’ versus ‘why?’ distinction corresponds to the distinction between causes on the one hand and reasons or ends on the other. However, Mayr is careful to provide an account of this teleological way of talking to avoid lapsing into an unscientific kind of finalism. ‘Teleology’ from the Greek ‘telos’ for “end” or “goal” refers to purposiveness. A hallmark of the scientific revolution was the rejection of ancient and medieval applications of teleological reasoning to the cosmos. In slogan form, physics progressed when it came to focus on causes rather than

purposes. Biology on the other hand, and evolutionary biology in particular, appears to require reasoning about what a given trait is for, or what good it does for the organism. Biological explanation appears to be ineliminably teleological, but according to dominant conceptions of scientific reasoning, teleological reasoning is unscientific. There appear to be three possible responses to this: 1) claim that biological explanation is not really teleological, 2) admit that biological explanation is not really scientific, or 3) claim that teleological reasoning can be scientific after all. Philosophers and scientists have tried all three, but Mayr argues that the class of processes that have been labeled as teleological are not unified and that a combination of all three strategies is necessary.

Mayr distinguishes four phenomena that have all traditionally been grouped under the heading of teleology. For reasons I will not try to explain Mayr believes it is less misleading to talk of processes being teleological rather than systems, so he defines four kinds of end-directed processes.³⁰ Teleomatic processes are those that simply converge on an end as a result of natural laws. Mayr's primary examples are the operations of gravity and the second law of thermodynamics. Teleonomic processes are those that are controlled by a program. I describe and defend Mayr's views on programs at length in a companion paper, but for now it is sufficient to note that programs provide a mechanistic explanation for how a system can be end directed. Mayr includes developmental and cognitive processes in this group, along with the operations of digital computers. Cosmic teleology is the kind of teleological process that science has eschewed. It would involve some sort of fundamental end-directedness in the universe. According to Mayr, cosmic teleology does not really exist, teleomatic processes are not really teleological because they have no true goal, and teleonomic processes are scientifically kosher—the theory of computation has shown us how that kind of teleology is mechanistically explicable.

Mayr's fourth category he calls adapted systems, breaking his rule of focusing on processes rather than systems, but we can translate this into the process of adaptation through natural selection. Natural selection occupies a place between teleomatic and teleonomic processes. On the one hand, like teleomatic processes, natural selection has no goal and is not the result of a program. But, like teleonomic processes, natural selection licenses or even requires teleological language and reasoning to fully describe. At several points, Mayr merely claims that teleological language and reasoning are a useful heuristic,³¹ but when he is actively criticizing reductionism, his claims are stronger, as they must be if the teleological character of evolutionary explanations is supposed to block reductionism. For Mayr, natural selection is "teleological" (scare quotes because his entire point is that the blanket term 'teleological' is misleading) enough to block reduction to the physical sciences, but not so teleological that it is unscientific.³²

Ultimate causes, according to Mayr, are a trait's contributions to fitness that explain why it was favored by selection. They can be invoked to answer 'why?' questions because they are "teleological" in some important sense, but not in the cosmic sense that science has discredited nor in the sense that they are directed by a program. Because the causes studied by lower level sciences lack this teleological character, evolutionary biology cannot be reduced to them. And, because developmental, mechanistic, and behavioral features of organisms, including those that by Mayr's own lights contribute to our understanding of evolutionary processes like speciation, are teleological in the sense that is explained by a program, evolutionary biology cannot be reduced to them either. A complete picture of mechanisms leaves unanswered the question of what effects of the trait explains why it has been favored by natural selection, even if indirectly, and this is true even if that trait is itself something like plasticity, evolvability, or dispositions to select particular habitats.

The "teleological" character of natural selection captures Mayr's basic strategy for blocking reductionism, but the story is incomplete. It is no case against reductionism to simply assert that

natural selection requires teleological reasoning or language in some way that precludes the physical sciences, or molecular biology, from capturing it and assure the reductionist that this does not represent lapse into cosmic teleology. Details are owed about what exactly about natural selection makes it special in this way, and Mayr has a story.

This part of Mayr's account tends to rely heavily on his notion of genetic program. Though I defend the cogency of genetic programs elsewhere, I will simply assume here for the sake of argument that the notion is coherent. The notion plays two important roles: 1) Recall that programs are essential to Mayr's distinction between teleonomic processes and selection. I will return to this point below. 2) According to Mayr, we must explain both how the program operates (proximate causes) and how it came to carry the specific information that it does (ultimate causes). Programs serve as a way for Mayr to emphasize the historical character of ultimate causes.

In the original 1961 formulation, Mayr notes that 'why?' questions can be interpreted as 'what for?' or as 'how come?' questions. He claims that the biologist always has in mind the 'how come?' question, so it appears that Mayr's view is that what appears teleological about natural selection is really historical. Many authors still emphasize this part of Mayr's formulation, and David Haig castigates researchers who erroneously treat ultimate explanations as answers to 'what for?' rather than 'how come?' questions.³³ However, in his 1982 Growth of Biological Thought, Mayr explicitly reverses his position on this characterization. "The question "why?" in the sense of "what for?" is meaningless in the world of inanimate objects. One can ask, "Why is the sun hot?" but only in the sense of "how come?" By contrast, in the living world the question "what for?" has powerful heuristic value."³⁴

Mayr's change of mind likely resulted from recognition that evolutionary biology is not alone in dealing with historical questions. As he notes in that same work, embryology, geology, and cosmogony all share this feature. However, Mayr continues to emphasize that ultimate causes are

historical, even using ‘historical’ as a proxy term for ‘ultimate’ in other parts of the book. Mayr recognized that simply pointing out that evolutionary biology is a historical science would not do to block reductionism, but he did not change his mind that ultimate explanations must be historical.

To understand the role history plays in Mayr’s framework, it is important to recognize that when Mayr says that explanations citing ultimate causes are historical, he means that they take the form of narratives.³⁵ Evolutionary biologists typically aim to explain events in the past over long timescales relative to human life spans, but neither being in the past nor long relative to human timescales is necessary for an explanation to be narrative in the relevant sense. Narrative explanations target single events rather than general laws or mechanisms. Narratives are not specific to evolutionary biology, or even to sciences that are historical in the sense that they are concerned with past events or long time-scales, like geology and cosmogony. However, Mayr emphasizes that evolutionary biology in particular is concerned to provide narratives for especially unique and complex events. In “Cause and Effect in Biology” Mayr notes that “In the uniqueness of biological entities and phenomena lies one of the major differences between biology and the physical sciences.” This point rears in his later writing on the proximate-ultimate distinction.³⁶

In his final 2004 book, What Makes Biology Unique, he makes the connection between ‘why?’ questions, narrative, and uniqueness explicit:

“Evolutionary biology is a historical science ... It deals, to a large extent, with unique phenomena, such as the extinction of dinosaurs, the origin of humans, the origin of evolutionary novelties, the explanation of evolutionary trends and rates, and the explanation of organic diversity. There is no way to explain these phenomena by laws. Evolutionary biology tries to find the answers to “why?” questions. ... With experiment unavailable for research in historical biology, a remarkable new heuristic method has been introduced, that of historical narratives.”³⁷

Here, as with his remarks about teleological language, we should not take Mayr's characterization of historical narrative as a heuristic to mean that he sees it as an eliminable shorthand. Mayr is clear that this methodological divide blocks the reduction of evolutionary biology to branches of biology concerned with proximate causes and to the physical sciences. However, it is not immediately clear how, given that Mayr recognizes—in this case in the very next paragraph—that other sciences also make use of historical narrative.

This puzzle can be solved with the help of a useful distinction Adrian Currie has drawn between simple and complex narratives.³⁸ A simple narrative explanation is the application of our understanding about a general mechanism or law to a particular case. Currie's primary example is the explanation of various geological data in terms of the snowball earth theory, according to which Earth's surface was completely glaciated. According to this theory, glaciation increased Earth's albedo (its tendency to reflect solar radiation back out into space) sufficiently to create a positive feedback loop, resulting in runaway cooling and glaciation. This narrative applies a general mechanism, albedo's effect on climate, to a specific case.

A complex narrative is not unified by a particular general mechanism. Currie notes that complex narratives rely on a specific, diffuse, and complex set of disparate explanans. Currie's primary example here is, tellingly, a biological one, sauropod gigantism. Paleontologists' explanation for why sauropod dinosaurs reached such large sizes compared to any other land animals in history relies on a complex array of mechanisms and specific, historically contingent events. The point is not that no general mechanisms or laws are invoked, but that “in a complex narrative, we appeal to regularities in order to support specific factors in the narrative—it is the narrative which carries the ‘explanatory load’. In simple narratives, the general model plays a unifying role, and it is the regularity which carries the explanatory load.”³⁹

At multiple points, including in “Cause and Effect in Biology,” Mayr emphasizes the complexity of biological phenomena, and the uniqueness of evolutionary phenomena. With the distinction between complex and simple narratives in mind, consider the following claims

- “Each mountain is unique; so is each weather system, and each planet and star. However, such uniqueness in the inanimate world is limited to complex systems, while the basic building blocks of these systems (elementary particles, atoms, molecules and crystals) consist of identical components. In the living world, uniqueness is seen even at the molecular level in the form of DNA or RNA.”⁴⁰
- “attempts to deny the importance of historical narratives or to axiomatize them in terms of covering laws fail to convince.”⁴¹

We have here a plausible difference between the kind of historical explanation that occurs in evolutionary biology and the kind that occurs in geology, cosmology, and even embryology. Currie suggests that there is a tension between reductive mechanistic explanation and complex narratives because complex narratives do not directly invoke the general laws that reductionism treats as necessary for explanatory adequacy. Mayr agrees. Note that Mayr, too, contrasts historical narrative with a search for laws, and the reason for the distinction is that historical narratives apply to unique events. Like Currie, Mayr does not think this is the case for all narratives. He does not extend this point to the narratives used in the physical sciences because the components of those systems are all alike. This would make sense if Mayr believes that the underlying uniformity of planets, stars, weather, systems, and mountains allows them to be subsumed under general laws in the form of simple narratives (though of course Mayr lacked that terminology).

This interpretation is also supported by Mayr’s claims in The Growth of Biological Thought about methodological differences between evolutionary biology and both the physical sciences and other branches of biology. First, Mayr claims that mathematics has little to no role to play in

evolutionary theory while it is essential to the physical sciences, and perhaps useful to some areas of biology. Second, he claims that the experimental method plays a relatively minor role in evolutionary biology compared to those other areas. Both of these methods are typically associated with formulating general laws. Mayr makes the very strong claim that mathematics plays no role in evolutionary theory, despite being fully aware of Fisher's mathematical models of genetic change. Fisher's sex ratio theory has been touted as one of the few cases of a general biological law.⁴² As Mayr was a staunch critic of Fisher's gene centered view of evolution that embodies the kind of reductionism Mayr was out to undermine, Mayr's dismissal of mathematical models may thus represent an indirect criticism rather than an oversight. In any case, Mayr's claims about the irrelevance of math and experimentation to evolutionary biology may have been overstated, but there is an important point here.

Note that Mayr does not need to claim that evolutionary biology never uses the methods of the physical sciences. But, he does need to cut off any temptation to view only those bits of biological theory that do approximate the physical sciences as the scientifically legitimate parts. Recall that half of his anti-reductionist case is to show that his anti-reductionism does not come at the price of scientific credibility. Mayr seems to treat the distinction as categorical, but he could consistently agree with Currie that narratives fall into a continuum of simple to complex and still argue that the role of complex narratives in evolutionary biology explain why it often requires different methods than those of the physical sciences, and non-evolutionary biology.

It is important to keep in view that while Mayr has a philosophical axe to grind with the focus of philosophy of science on physics, his more immediate practical aim is to block the view that biology could become a "real science"—read, more like physics—by reducing all biology to molecular biology. The link I have established between Mayr's views and functional analysis as explicated by Cummins largely solves the problem of reductionism to the minds of many current

philosophers. But, Mayr either did not recognize or did not agree that merely invoking functions is enough. I suspect the latter. Mayr recognizes that there are multiple senses of reduction, and he takes the distinction between reduction and analysis to block *explanatory* reductionism, which Mayr takes to be the view that to understand a system one must break it down to its smallest components.⁴³ However, he makes a separate case against *theory* reductionism, the view that the theories and laws of one science are a special case of theories and laws of another.⁴⁴

Mayr claims that theory reduction confuses laws with concepts and specifically gives the example that “any adapted structure is the result of selection, but this again is a concept which cannot be expressed in strictly physico-chemical terms.”⁴⁵ This paired with Mayr’s defense of organisms rather than genes as the units of selection and rejection of definitions of evolution in terms of changes in gene frequency,⁴⁶ make it reasonable to think Mayr’s real target when he emphasizes the historical character of ultimate explanations is theory reduction, especially theory reduction of evolutionary biology to molecular biology. To undermine theory reduction, Mayr needs something that sets evolutionary biology apart from other areas of biology, and he sees complex narratives as the thing that does the trick.

Mayr emphasizes the importance of this separation *within* biology not only in his distinction between evolutionary and functional biology in his initial presentation of the proximate-ultimate distinction but also specifically in the context of his discussion of narratives.

“The methodology of historical narratives is clearly a methodology of historical science. Indeed evolutionary biology as a science, in many respects is more similar to the Geisteswissenschaften than to the exact sciences. When drawing the borderline between the exact sciences and the Geisteswissenschaften, this line would go right through the middle of biology and attach functional biology to the exact sciences while classifying evolutionary biology with the Geisteswissenschaften. This,

incidentally, shows the weakness of the old classification of the sciences, which was made by philosophers familiar with the physical sciences and the humanities but ignorant of the existence of biology.”⁴⁷

‘Geisteswissenschaften’ is a German term that translates roughly to “humanities”, and the glossary of Mayr’s book confirms that this is his meaning. Interestingly, he uses the German terminology in a book written in English meant to be accessible to a popular audience. This suggests the terminology is playing a deeper role. It may indicate that Mayr is channeling earlier Neo-Kantian’s who argued for a very similar view, namely that what separates the Geisteswissenschaften from the exact sciences, the Naturwissenschaften, is that the former concerns unique narratives.⁴⁸ I have been unable to locate an explicit reference to the neo-Kantians but Mayr’s approving remarks about Kant’s recognition of the irreducibility of teleological processes to physical processes makes the interpretation all the more plausible.⁴⁹ In Mayr’s view, Kant’s only mistake was to be overly pessimistic about there being a “Newton for teleology” because it turned out Darwin was just that.

The connection with the neo-Kantians also helps to explain the connection between unique historical narratives and teleology, and hence why both together characterize ultimate causes. One of the puzzles about functional explanation is why they do not typically occur in the physical sciences. The usual argument against reductionism from the nature of functional explanation emphasizes the multiple realizability of functionally characterized systems. The same function may be served by different physico-chemical underpinnings. But, this does not explain why biology and other sciences dealing with living systems invoke functional explanations and physics does not. The case against reductionism is incomplete unless it can be shown that functional explanation is both scientifically kosher and necessary for biology but not the physical sciences. “Teleology” (again in the general sense Mayr takes to be

ambiguous) provides an answer. Only “teleological” systems call for the kind of means to ends reasoning invoked in functional explanation. Just as Kant argued, biology but not physics requires this sort of reasoning; however, the neo-Kantians provided a way to link teleological reasoning to place this reasoning in the empirical realm without abandoning Kant’s insight.

Here Mayr’s emphasis on genetic programs pulls some theoretical weight. Mayr claims at several points that the proximate-ultimate distinction somehow arises from the fact that living systems are governed by programs, but he never explicitly states in what sense programs explain why there is a distinction between proximate and ultimate causes. But, programs mark the boundary between two different types of “teleology.” This fact is important for seeing why the proximate-ultimate distinction marks a boundary within biology, not just between biology and the physical sciences.

Mayr is clear that the operations of a program are a proximate cause for end-directed behavior.⁵⁰ The motivation for Mayr invoking programs at all is precisely that they provide the only known non-mysterious mechanism for truly goal directed behavior. The end-directedness of biological processes like development, behavior, cellular replication, and molecular processes calls for functional explanation because they are end-directed, and this separates biology in general from the physical sciences. But, the end-directedness of these processes is scientifically kosher, unlike cosmic teleology, because it can be explicated in terms of the underlying physical processes implementing a program. And, this explanation is not historical. Mayr explicitly rejects any historical characterization of programs.⁵¹

Evolutionary biology is different. Mayr takes pains to emphasize that it is not truly end-directed. It is not rendered scientifically acceptable by assimilation to the physical sciences via the operation a program but through a complex narrative showing how a

plethora of disparate physical processes can act in concert to produce the fit between means and ends that makes functional explanation indispensable.

Mayr's labeling of teleological language as heuristic provides a clue about Mayr's views on the methodological connection between complex narrative and teleological language. Given that the ingredients in a complex narrative can arise from highly disparate sources, historical science needs a method for searching the possibility space for relevant considerations. For Mayr, this method is adaptationism, or the search for selective advantages. Teleological language, on this interpretation, carries none of the explanatory load—to borrow Currie's terminology—but it provides a unifying principle that guides the construction of complex narratives. That is, teleological reasoning allows biologists to wade through the multiplicity of possible physical processes that might be relevant to home in on the selective advantage at work, and this in turn guides the construction of the narrative through analysis of the mechanisms underlying that selective advantage and the source of the variation necessary for selection to act. It may be possible to state a particular narrative without recourse to teleological language, but without teleological reasoning we would most likely never stumble on the right narrative, and we would miss what unifies the many disparate narratives comprising our picture of the history of life.

This last point is more speculative than the rest, but whether or not this interpretation is correct, Mayr clearly believes that ultimate explanations are both historical and invoke natural selection. Either alone is not sufficient: Recall Mayr's claim that evolutionary biology sometimes asks 'how?' questions, for example asking how species multiply.⁵² Only those evolutionary narratives that specifically invoke natural selection count as ultimate explanations. Though Mayr originally flirts with the idea of reducing teleological language to history, his mature view is that the teleological and historical character of many, but not all, evolutionary explanations are separate features that together

block reductionism. “Teleology” supports a kind of autonomy of biology from the physical sciences, but the specific way in which the teleological language is underpinned by historical narratives rather than programs separates evolutionary biology from other areas of biology.

It is now possible to say more explicitly how the standard model, according to which ultimate causes are those cited to answer Tinbergen’s questions about survival value and evolution, is too simple. As Tinbergen argues, information about survival value is useful for constructing historical narratives, but even if organisms had just been created by a powerful deity, we would still want to know how they manage to survive. And, that a trait contributes to survival in a particular way currently does not imply immediately that selection is or was at work. We need more information to make this inference.⁵³ On Mayr’s view, elucidation of a trait’s contribution to survival value only counts as an elucidation of ultimate causes if that contribution is part of a narrative explanation somehow involving selection. This point also shows the flaw in several critics’ claim that Mayr errs in thinking of ultimate causes as causes at all because functions are not causes.⁵⁴ Mayr only recognizes as ultimate causes only those contributions to survival and reproduction that occur in a causally explanatory narrative of actual evolutionary change or maintenance. Ultimate causes, are indeed causes.

This does not imply that ultimate causes can only explain a trait’s origins. It can be a narrative about current maintenance of the trait or about probable future evolution, as when conservation biologists attempt to predict plausible selective responses to climate change or intervention on an invasive species. Similarly, a historical narrative of a trait’s evolution does not count as ultimate if that narrative does not invoke natural selection. Change due to drift or mutation, or persistence due to lack of variation, do not answer ‘why?’ questions—that is are not “teleological”—and thus are not ultimate causes. I suspect that Mayr believes that these processes might be reducible to molecular and physical, and in any case, he could consistently maintain that

they could be since his project does not require that *no* evolutionary explanations are reducible. Nor, I will argue, does Mayr class evolutionary changes due to non-selective processes as proximate explanations. He countenances a third category, under what he calls the “role of chance.”

6. The Role of Chance and Population Thinking

Along with teleology, Mayr always juxtaposes discussion of the proximate-ultimate distinction with discussion of the role of chance in biology. Mayr’s most obvious reason for doing so is that emphasizing the role of stochastic processes in biology allows him to answer critics who claim that biology does not meet the standards of science because it is unable to make predictions about many biological phenomena, like the course of future evolution. However, Mayr’s conception of the role of chance also shows that Mayr does not believe that all evolutionary explanations are ultimate explanations.

Mayr often uses the terms like ‘chance’ and ‘randomness’ in a somewhat idiosyncratic way, at least with respect to usage outside of biology. Though Mayr sometimes notes that the stochastic nature of biological processes is important, in the context of the proximate-ultimate distinction Mayr claims that randomness or chance in the biological sense is not a matter of being indeterministic but rather of lacking purposiveness or direction. ‘Random’ Mayr says means “not a response to an adaptational need of the organism.”⁵⁵ Chance is opposed to selection in that the latter but not the former is *directional*, and this directionality is characterized by non-accidental fitness increase.

Natural selection, Mayr emphasizes, is a two-step process. The first step is variation, and the second, he calls “selection proper.”⁵⁶ This is important, because while Mayr argues throughout his work that it is essential to understand the origins of variation to fully understand the evolution of a trait, only “selection proper” is an ultimate cause. In fact, it is the only evolutionary cause Mayr countenances: “Directional causes are caused by natural selection, but constrained by the potential of the existing genotype.”⁵⁷ He makes a distinction between causes and constraints, and under the

heading of constraints includes phenotypic plasticity, lack of variation, developmental canalization, “evolutionary noise” (I suspect he has drift and repeated mutation in mind here), cohesion of the genotype and developmental system, and limited potential of a particular body plan (bauplan).⁵⁸

Mayr’s specific usage of the term ‘chance’ to mean ‘non-goal-directed’ rather than ‘non-deterministic’ leaves open the possibility of mechanistically explaining patterns in non-selective, “chance” processes through analysis. If we start with the tendencies of populations and lineages to change and persist, as I suggested in Section 4, both Mayr and Tinbergen agree that we can apply functional analysis to break this tendency down into more basic dispositions, and as part of this process we will move between levels of organization. In principle, the process can continue down to the level of the most general dispositions, that is laws, governing the activity of the most basic categories recognized by the physical sciences. However, Mayr cautions us that below a certain level of organization, this task is no longer illuminating. The uniqueness of biological phenomena renders the task pointless in many cases.

This kind of analysis includes tracing out how mechanisms and development give rise to the variation on which selection acts, how individuals in a population change over time, and much else that recent integrative research projects have sought to accomplish. However, Mayr and Tinbergen both rejected reductionism in the form of claims that elucidating mechanisms precludes the need to ask questions about selection. As Tinbergen phrases it “the biology of behavior is more than the physiology of behavior just as biology is more than physiology.”⁵⁹

Mayr also emphasized that evolutionary explanations, including those that cite non-ultimate causes, must occur at the level of populations because evolution is a population-level process. André Ariew argues the distinction between individual and population level processes is the only useful component of the proximate-ultimate distinction.⁶⁰ However, being at the population level does not imply that a process is teleological or historical in the senses important to Mayr’s philosophical

project, so Ariew is largely missing Mayr's point. But, Ariew is correct that the distinction between population and individual level processes is important for understanding Mayr's proximate-ultimate distinction. Mayr's emphasis on the importance of what he calls population thinking for understanding evolution explains how he conceives of the relationship between ultimate causes and other factors relevant to evolutionary explanations.

Mayr defends the view that Darwin's primary insight was a move away from essentialist, or typological, thinking to population thinking. Evolution is a population level phenomenon, but populations are made up of individuals, and in particular individuals that experience developmental change. Through analysis, individual level features can contribute to our understanding of population level processes. Developmental, mechanistic, and even physico-chemical laws and causes can contribute to evolutionary explanation through analysis, but this means saying how it is that those processes and causes are organized such that *at a population level* they manifest as either selection, or one of the many constraints on selection Mayr recognizes. That is, at the population level, individual level causes will constitute part of an analysis of either selection itself, the role of chance, or both. But, again, only those causes cited in a historical narrative of selection pressures count as ultimate, because those are the ones that Mayr invokes to block reductionism.

7. Mayr's Criticism of Evo-Devo

This leaves a final puzzle. I have argued that biologists and philosophers who see the proximate-ultimate distinction as a barrier to integration have misinterpreted Mayr's philosophical project, but many have claimed that Mayr himself explicitly rejects integrative projects, evo-devo in particular. I have argued that Mayr explicitly endorses invoking non-ultimate causes to explicate evolutionary processes and history, and that the proximate-ultimate distinction, properly interpreted, does not rule it out. How are we to interpret Mayr's criticism of evo-devo, or as one commentator put it "Mayr's insistence that development is irrelevant to evolution?"⁶¹

In short, Mayr never insists on the irrelevance of development to evolution. I have provided several quotes from him showing unequivocally that he accepted the relevance of development to evolution. Ron Amundson argues that because Mayr never says how development could be relevant to evolution without conflating proximate with ultimate, Mayr must have thought development irrelevant to evolution.⁶² Since I have explained exactly how this is possible, the problem is solved, but it is worth noting that Mayr likely provided no explicit characterization because he, unlike his critics, never thought the proximate-ultimate distinction represented any barrier to integration.

I have not been able to find anything that looks like a rejection of the relevance of development to evolution, but critics have cited two particular works. I have already noted the following quote from one of those sources above.

“Those developmental biologists who will work on this problem, together with the molecular biologists, will certainly make a far greater contribution to our understanding of evolution than those who present to the world a completely erroneous picture of the current beliefs of the Darwinians.”⁶³

I quoted this passage in Section 3 to show that Mayr explicitly allows for developmental biology to make contributions to our understanding of evolution, so it is unclear how this work could be interpreted as an argument for the irrelevance of development to evolution. Rather, Mayr’s primary target is what he sees as misrepresentations of the modern synthesis. In particular Mayr targets M.W. Ho and P.T. Saunders, claiming that they misrepresent the modern synthesis by equating it with Fisher’s population genetics and a gene-centric definition of evolution, the very one Mayr had spent many years criticizing. However, he also criticizes those authors for conflating proximate and ultimate.

Note that in the other source, a 1992 essay called “Controversies in Retrospect,” Mayr simply refers back to the points he made in the 1984 article I have quoted and reiterates that these researchers have wrongly characterized the modern synthesis. And, he summarizes the controversy by noting that “some developmental biologists still attack the synthesis because of its support for Darwinian variational rather than developmental transformational evolution.”⁶⁴

Mayr’s claims that one particular pair of authors have conflated proximate-and ultimate and that some developmental biologists have objected to the modern synthesis in a way that he sees as mistaken hardly constitutes a rejection of the relevance of developmental biology to evolution. This alone is enough to show that the view that Mayr had some sort of general, in principle, problem with development contributing to evolutionary explanation is unfounded, but understanding where he thinks *some* developmental biologists have erred reveals more about Mayr’s conception of the proximate-ultimate distinction.

Transformational evolution, according to Mayr, is the view “first clearly articulated by Lamarck” that “evolution consists of the gradual transformation of organisms from one condition of existence to another.”⁶⁵ He notes that it typically conceives of evolution as an inevitable trend to a particular goal or ultimate state of perfection. In short, Mayr thinks some of his critics are out to revive a discredited Lamarckian view of evolution as goal-directed. In the 1984 paper, Mayr specifically links his claim that Ho and Saunders have confused proximate and ultimate to their claim that “constraints to form thus arise as a natural necessity rather than from natural selection.”⁶⁶ Mayr is likely reading “natural necessity” here as “cosmic teleology” and his reading is encouraged by Ho and Saunder’s explicit approving invocation of Lamarck.⁶⁷ Ho and Saunders, on Mayr’s view, have conflated proximate and ultimate in the same sense that Lamarck did in thinking that individual

developmental systems strive toward some goal, guided by some *sui generis* end-directedness, that is then inherited and continued with each generation. That is, they have taken a description of developmental mechanisms alone to explain *directional* evolutionary change independently of any appeal to selection. Note that Mayr is not rejecting the role of the availability of variation to direct evolution in the sense of constraining the options available for selection, but the view that there is an intrinsic and basic goal-directedness in living systems—that is, vitalism. I suspect that what is at issue is whether any sense can be made of “laws of form” that lead to directional changes without explaining those laws themselves as the result of selection. My own suspicion, and Mayr’s is that the answer is no. This is not to say that there are no laws of form, only that they are not both *sui generis* and goal-directed.

However, note that answering no to this question is compatible with development contributing to evolutionary explanations. Some biologists have argued that developmental mechanisms of salamander limb development enforce a correlation between digit number and overall body size.⁶⁸ This is an individual level, proximate, developmental explanation but it can contribute to our understanding of evolution by explaining a lack of variation in salamander populations. Note that we cannot immediately infer this lack of variation by simply noting the details of the mechanism. Selection may maintain the developmental correlation through direct selection or through selection against other phenotypic consequences of variations that would break the correlation. The ultimate causes in this case would be the selective role of that phenotypic effect. Elucidating the mechanism does not answer the question about which selective process is at work, or whether one is. Inferring immediately that selection has not acted or that some particular selective advantage was at work, knowing only the details of the developmental mechanism, would be to conflate proximate and ultimate. This is a mistake that I believe some have made.⁶⁹ More importantly

for present purposes, it is consistent to claim that someone conflates proximate and ultimate causes without completely rejecting the relevance of their findings to evolutionary theory.

Imagine we add additional evidence favoring the hypothesis that variation has not occurred, for example several optimality models demonstrating that smaller salamanders have fewer digits than what selection should favor, even accounting for possible developmental effects elsewhere in the system. Whatever the explanation for this lack of variation, as long as the variation is not directed such that it non-randomly increases fitness (and if the source of evidence is deviation from optimality models, we have evidence it is not), then at the population level this falls under the heading of the role of chance, in Mayr's specific sense. Still, the developmental mechanism contributes to evolutionary explanation, because it provides an analysis of a particular constraint on selection. So far, there's nothing at odds with Mayr's views or the proximate-ultimate distinction. There is only a conflict if the claim is that the change non-accidentally fitness-conducive but not the result of selection in some form, even indirectly through selection on a linked phenotypic effect. I see no reason integrative research needs to posit "teleology" (in Mayr's broad, ambiguous sense) capable of producing a fit of means to ends that is not explained by selection or programs. Those who disagree have the burden of explain what this force or process is, and simply using the phrase "law of form" is no explanation.

8. Conclusion

The standard view says that Mayr's and Tinbergen's frameworks are essentially the same, with Tinbergen's four questions simply subdividing Mayr's proximate-ultimate distinction. Ultimate causes are invoked to answer 'why?' questions and proximate causes to answer 'how?' questions. Tinbergen's evolutionary and survival value questions are 'why?' questions while his mechanistic and developmental questions are 'how?' questions. This leads to a puzzle about how we could integrate

the questions, because the proximate-ultimate distinction is supposed to mark a categorical divide that blocks the reduction of evolutionary biology to other forms of biology. I have argued that the standard picture is incorrect, and that there is no conflict between the proximate-ultimate distinction and integration of Tinbergen's four questions.

To this end, I have argued that both Tinbergen's and Mayr's conception of integration is captured by Robert Cummins's account of functional analysis. The four questions represent different perspectives we can take on a single causal system in relation to behavior. There is a distinction between evolutionary and survival value questions on the one hand and mechanistic and developmental questions on the other. The former takes an upward looking functional perspective from which we think of a behavior in the larger context of a population, while the latter takes a downward looking decomposition of the behavior. However, this distinction is not the proximate-ultimate distinction.

The proximate-ultimate distinction represents a combination of historical and teleological features, with neither reducing to the other, unique to natural selection that Mayr argues blocks the reduction of evolutionary theory to either physics or to other areas of biology like molecular biology. The ability of selection to bring about a fit between ends and means, a feature shared by all biological systems, makes functional explanation ineliminable, unlike in the physical sciences. However, this teleological character is explained by historical narratives in evolutionary biology but by the operation of programs in other areas. This marks a methodological divide, according to Mayr, between evolutionary biology and other areas of biology, with proximate biology more closely approximating the methods of the physical sciences.

This is all compatible with Mayr's overt recognition that proximate causes can contribute to evolutionary explanations. Not all causes cited to explain survival value or evolutionary history count as ultimate, only those that occur as part of a narrative invoking natural selection. This leaves two

paths for non-ultimate causes, including not only proximate causes but also non-biological physico-chemical causes, to contribute to evolutionary explanations. Those causes might be part of an analysis of selection itself, but this does not make them ultimate causes. Alternatively, they may occur in an analysis of a constraint on evolution, and therefore fit into Mayr's third category, "the role of chance," which encompasses all evolutionary processes that do not have selection's ability to fit ends to means.

This analysis reveals the relationship between Mayr's and Tinbergen's frameworks to be more complicated than most biologists and commentators have taken it to be. The pay-off is that it relieves the tension between Tinbergen's call of integration and Mayr's case for autonomy and provides a more philosophically nuanced and historically defensible interpretation of both.

Notes

¹ Ernst Mayr, "Cause and Effect in Biology," *Science*, 134, 3489, (November 1961): 1501-1506; Ernst Mayr, "Teleological and Teleonomic: A New Analysis," *Boston Studies in the Philosophy of Science*, 14, (1974): 91-117; Ernst Mayr, *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, (Cambridge, MA: Harvard University Press, 1982); Ernst Mayr, "The Triumph of the Evolutionary Synthesis," *Times Literary Supplement*, 4257, (November 1984): 1261-1262; Ernst Mayr, *Toward a New Philosophy of Biology: Observations of an Evolutionist*, (Cambridge, MA: Harvard University Press, 1988); Ernst Mayr, "The Idea of Teleology," *Journal of the History of Ideas*, 53, 1, (January-March 1992): 117-135; Ernst Mayr, "Proximate and Ultimate Causations," *Biology and Philosophy*, 8, 1, (January 1993): 93-94; Ernst Mayr, "The Autonomy of Biology: The Position of Biology among the Sciences," *The Quarterly Review of Biology*, 71, 1, (March 1996): 97-106; Ernst Mayr, *This is Biology: The Science of the Living World*, (Cambridge, MA: Harvard University Press, 1997); Ernst Mayr, *What Makes Biology Unique: Considerations of the Autonomy of a Scientific Discipline*, (Cambridge, MA: Harvard University Press, 2004).

² Niko Tinbergen, "On the Aims and Methods of Ethology," *Zeitschrift für Tierpsychologie*, 20, 4 (1963): 410-433.

³ Paul W. Sherman, "The Levels of Analysis," *Animal Behavior*, 36, 2, (April 1988): 616-619; Kay E. Holecamp and Paul W. Sherman, "Why Male Ground Squirrels Disperse," *American Scientist*, 77, 3, (May-June 1989): 232-289; John Alcock, *Animal Behavior: An Evolutionary Approach*, 7th ed., (Sunderland, MA: Sinauer 2001); Scott A. MacDougall-Shackleton, "The Levels of Analysis Revisited," *Philosophical Transactions of the Royal Society B, Biological Sciences*, 366, 1574, (July 2011): 2076-2085; Patrick Bateson and Kevin Laland, "Tinbergen's Four Questions: An Appreciation and

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⁴ John Beatty, “The Proximate/Ulimate Distinction in the Multiple Careers of Ernst Mayr,” *Biology and Philosophy*, 9, 3, (July 1994): 333-356; Ernst Mayr, “Response to John Beatty,” *Biology and Philosophy*, 9, 3, (July 1994): 357-358.

⁵ Ernst Mayr, “Cause and Effect in Biology,” *op. cit.*

⁶ Tinbergen, “On the Aims and Methods of Ethology,” *op. cit.*

⁷ Julian Huxley, *Evolution: The Modern Synthesis*, (London: Allen & Unwin, 1942).

⁸ Tinbergen, “On the Aims and Methods of Ethology,” *op. cit.*

⁹ Ernst Mayr, “The Triumph of the Evolutionary Synthesis,” *op. cit.*; Sherman, “The Levels of Analysis,” *op. cit.*; Johan Bolhuis, “Function and Mechanism in Neuroecology: Looking for Clues,” *Animal Biology*, 55, 4, (2005): 457-490; Thomas C. Scott-Phillips, Thomas E. Dickins, and Stuart A. West, “Evolutionary Theory and the Ultimate-Proximate Distinction in the Human Behavioral Sciences,” *Perspectives on Psychological Science*, 6, 1, (January 2011): 38-47; Stuart A. West, Claire El Mouden, and Andy Gardner, “Sixteen Misconceptions About the Evolution of Cooperation in Humans,” *Evolution and Human Behavior*, 32, 4, (July 2011): 231-262; Thomas E. Dickins and Qazi Rahman, “The Extended Evolutionary Synthesis and the Role of Soft Inheritance in Evolution,” *Proceedings of the Royal Society B, Biological Sciences*, 279, 1740 (August 2012): 2913-2921; Mark Fedyk, “How (not) to Bring Psychology and Biology Together,” *Philosophical Studies*, 172, 4, (April 2015): 949-967.

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- ¹² Gardner, "Ultimate Explanations Concern Adaptive Rationale for Organism Design," *op. cit.*
- ¹³ David Haig, "Proximate and Ultimate Causes: How Come? And What For?," *Biology and Philosophy*, 28, 5, (September 2013): 781-786; Kevin N. Laland et al., "More on How and Why: A Response to Commentaries," *Biology and Philosophy*, 28, 5, (September 2013): 793-810; Jerry A. Hogan, "A Framework for the Study of Behavior," *Behavioral Processes*, 117, (August 2015): 105-113.
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- ¹⁵ Robert Cummins, "Functional Analysis," *The Journal of Philosophy*, 72, 20 (November 1975): 741-765
- ¹⁶ Peter Godfrey-Smith, "Functions: Consensus Without Unity," *Pacific Philosophical Quarterly*, 74, 3 (September 1993): 196-208.
- ¹⁷ C.f. Donald Dewsbury, "The Proximate and the Ultimate: Past, Present, and Future," *Behavioral Processes*, 46, 3, (July 1999): 189-199.
- ¹⁸ Ernst Mayr's Letters and Correspondence, Harvard University Archives, Manuscript.
- ¹⁹ Ernst Mayr, "The Triumph of the Evolutionary Synthesis," *op. cit.*
- ²⁰ Ernst Mayr, *What Makes Biology Unique: Considerations of the Autonomy of a Scientific Discipline*, *op. cit.*
- ²¹ *Ibid.*
- ²² Ernst Mayr, "The Triumph of the Evolutionary Synthesis," *op. cit.*, Ernst Mayr, *Toward a New Philosophy of Biology: Observations of an Evolutionist*, *op. cit.*; Ernst Mayr, *What Makes Biology Unique: Considerations of the Autonomy of a Scientific Discipline*, *op. cit.*
- ²³ Ernst Mayr, *What Makes Biology Unique: Considerations of the Autonomy of a Scientific Discipline*, *op. cit.*
- ²⁴ *Ibid.*
- ²⁵ Ernst Mayr, *Animals, Species, and Evolution*, (Cambridge, MA: Harvard University Press, 1963).

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- ²⁷ Cummins, *The Nature of Psychological Explanation*, *op. cit.*
- ²⁸ Tinbergen, "On the Aims and Methods of Ethology," *op. cit.*
- ²⁹ Cf. Carl Craver, "Functions and Mechanisms: A Perspectivalist View" in P Huneman (ed.) *Functions: Selection and Mechanisms*, (Dordrecht: Springer, 2013).
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- ³¹ Ernst Mayr, *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, *op. cit.*; Ernst Mayr, *Toward a New Philosophy of Biology: Observations of an Evolutionist*, *op. cit.*
- ³² C.f. Vassiliki Betty Smocovitis, "Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology," *Journal of the History of Biology*, 25, 1, (Spring, 1992): 1-65.
- ³³ Haig, "Proximate and Ultimate Casues: How Come? And What For?," *op. cit.*
- ³⁴ Ernst Mayr, *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, *op. cit.*, 72.
- ³⁵ Ernst Mayr, *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, *op. cit.*
- ³⁶ See especially Ernst Mayr, *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, *op. cit.*
- ³⁷ Ernst Mayr, *What Makes Biology Unique: Considerations of the Autonomy of a Scientific Discipline*, *op. cit.*, 32.
- ³⁸ Adrian Mitchell Curie, "Narratives, Mechanisms, and Progress in Historical Science," *Synthese* 191, 6, (April 2014): 1163-1183.
- ³⁹ *Ibid.*
- ⁴⁰ Ernst Mayr, *Toward a New Philosophy of Biology: Observations of an Evolutionist*, *op. cit.*, 16.
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- ⁴⁵ Ernst Mayr, *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, *op. cit.*, 62.

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- ⁴⁶ See especially Mayr, *Animals, Species, and Evolution*, *op. cit.* and Mayr, *Toward a New Philosophy of Biology*, *op. cit.*
- ⁴⁷ Ernst Mayr, *What Makes Biology Unique: Considerations of the Autonomy of a Scientific Discipline*, *op. cit.*, 33.
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- ⁴⁹ Ernst Mayr, *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*, *op. cit.*; Ernst Mayr, *Toward a New Philosophy of Biology: Observations of an Evolutionist*, *op. cit.*
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- ⁵¹ Ernst Mayr, *Toward a New Philosophy of Biology: Observations of an Evolutionist*, *op. cit.*, 45.
- ⁵² Ernst Mayr, *What Makes Biology Unique: Considerations of the Autonomy of a Scientific Discipline*, *op. cit.*
- ⁵³ Tinbergen, "On the Aims and Methods of Ethology," *op. cit.*; c.f. John Endler, *Natural Selection in the Wild*, (Princeton: Princeton University Press, 1986).
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- ⁵⁵ Ernst Mayr, "The Triumph of the Evolutionary Synthesis," *op. cit.*
- ⁵⁶ Ernst Mayr, *This is Biology: The Science of the Living World*, *op. cit.*, 188; and in somewhat different words, Ernst Mayr, *Toward a New Philosophy of Biology: Observations of an Evolutionist*, *op. cit.*, 98.
- ⁵⁷ Ernst Mayr, *Toward a New Philosophy of Biology: Observations of an Evolutionist*, *op. cit.*, 109.
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