How-Possibly Explanation in Biology: Lessons from Wilhelm His's 'Simple Experiments' Models

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A common view of how-possibly explanations in biology treats them as explanatorily incomplete. In addition to this interpretation of how-possibly explanation, I argue that there is another interpretation, one which features what I term "explanatory strategies." This strategy-centered interpretation of how-possibly explanation centers on there being a different explanatory context within which how-possibly explanations are offered. I contend that, in conditions where this strategy context is recognized, how-possibly explanations can be understood as complete explanations. I defend this alternative interpretation by analyzing the explanatory value of simple physical models the nineteenth century developmental biologist Wilhelm His constructed for animal development.

Keywords

explanation • how-possibly • why-necessary • developmental biology • Wilhelm His

1 Introduction

The notion of how-possibly explanations emerged with William Dray (1957) in response to Carl Hempel's (1965) influential deductive-nomological (D-N) model of scientific explanation. Dray's aim was to distinguish explanations of states of affairs that might (merely) occur, in contrast to the aim of D-N explanations working to establish that states of affairs must actually occur. More recently, interest in how-possibly explanations has been particularly keen among philosophers of biology. One of the concerns philosophers of biology have focused on is whether how-possibly explanations are "complete" explanations. Dray considered how-possibly explanations to be complete explanations, but the view that they are incomplete explanations became prominent with Robert Brandon's (1990) articulation of successful adaptation explanation in evolutionary biology. According to Brandon, how-possibly adaptation explanations are incomplete, since they lack the requisite empirical evidence. Moreover, Brandon's characterization of how-possibly explanation can be seen as having set the stage for thinking broadly about how-possibly explanations in biology. Echoing Brandon's account for adaptation explanations, for

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example, David Resnik (1991) contends that how-possibly explanations are inherently incomplete, and yet they serve an important heuristic role throughout biology by setting out an agenda for future research.

Despite common acceptance of the view that how-possibly explanations are incomplete explanations, there has been some interest in recovering Dray's original position that they can be complete explanations (e.g., Forber 2010). My aim in this essay is to articulate a new approach for understanding how-possibly explanations as complete explanations.

The essay divides into two parts. The first part is an attempt to return to a basic insight that Dray had in introducing the notion of how-possibly explanation, an insight focused on the context in which how-possibly explanations are offered. Building on Dray's position, I argue that a proper understanding of how-possibly explanation requires explicating two distinct explanatory contexts. In this first part of the paper I work to demonstrate that the view that how-possibly explanations are incomplete explanations presumptively restricts explanatory practice to the first of these explanatory contexts. I contend, however, that the introduction and recognition of the second explanatory context offers an opportunity to see certain how-possibly explanations as complete explanations.

In the second part of the paper, I aim to illustrate the significance of the second explanatory context to how-possibly explanation by introducing a case study from the history of developmental biology. Specifically, I offer a brief summary of Wilhelm His's "simple experiments" research in which His attempted to construct rudimentary physical models of animal development. I argue that one dividend of His's simple-experiments models is its ability to illustrate the second of my explanatory contexts, and, correspondingly, it is particularly useful in demonstrating the way in which how-possibly explanations in biology can, in some instances, be characterized as complete explanations.

2 The Purported Incompleteness of How-Possibly Explanation and a Return to Dray

Perhaps the most fruitful place to begin a discussion of how-possibly explanation in biology is with Robert Brandon's (1990) characterization of them as incomplete adaptation explanations. Brandon's view is especially useful as an introduction to how-possibly explanation in biology, since he couples his understanding of how-possibly explanation to a detailed accounting of the criteria for a successful adaptation explanation. Brandon's account of successful adaptation explanations reveals, in turn, why it is that how-possibly explanations are supposed to be incomplete explanations.

On Brandon's view, the difference between how-possibly and how-actually explanations stems from their respective degrees of evidential support. How-possibly and how-actually explanations are distinguishable by the former being partially supported by the right sort of evidence, while the latter is fully supported by the necessary evidence. Since the difference between how-possibly and how-actually explanations is measured by degree of evidential support, those explanations that are only partially supported by available evidence should be characterized as incomplete explanations.

Naturally, a judgment that some explanations are incomplete based on their lacking evidential support requires articulating some criteria for measuring the kind and degree of evidential support needed to satisfy the demands for completeness.[1] To that end, Brandon offers the con-

[1]It might be worthwhile to note at this point that the "completeness" of how-possibly explanations may invite some initial confusion. Reference to "complete" explanation may conjure overwhelming demands, requiring an

cept of an ideally-complete adaptation explanation. Brandon goes on to outline five different types of evidence needed in support of an adaptation explanation, in order for it to be ideally complete: (1) evidence that selection has occurred on the relevant traits; (2) an ecological explanation of that selection; (3) an account of the underlying genetics of the traits (at minimum, evidence that the relevant traits are heritable); (4) information on population structure (in particular on patterns of gene flow and selective heterogeneity); and (5) phylogenetic information on trait polarity—that is, on which trait values are evolutionary primitive and which are derived. Adaptation explanations satisfying a subset of these criteria without satisfying the full complement are, by implication, incomplete. These incomplete adaptation explanations provide how a trait possibly arose, but they fail to account for how it actually arose.

Brandon's account of how-possibly explanations as it relates to evolutionary adaptations offers a particularly fruitful account for understanding their nature. For my purposes here, the most significant element of Brandon's account is that it represents a compelling case that there is a sense of how-possibly explanation which implies they are incomplete explanations. Moreover, the core element of Brandon's account for thinking about how-possibly explanations as incomplete explanations (i.e., the focus on degree of evidential support) might plausibly be extended to other areas of biology. To be sure, Brandon's account is somewhat restricted insofar as the incompleteness is due solely to evidence for an explanation rather than an incomplete set of explanatory factors themselves. But it's possible to acknowledge this distinction and remain committed to the fundamental point about how-possibly explanations being incomplete generally. David Resnik (1991), for instance, surveys what he takes to be a wide array of how-possibly explanations in biology. All of the examples Resnik considers from biology are incomplete explanations, but most concern an incomplete set of explanatory factors rather than a lack of supporting evidence for an explanation. Despite their incompleteness, however, Resnik argues for the explanatory significance of how-possibly explanations by demonstrating that they serve a heuristic role within biological practice.

The conceptualization of how-possibly explanations as incomplete and heuristically useful is noticeably prevalent among other philosophers of biology. Alexander Rosenberg (2006), for instance, frames his reductionist thesis for developmental biology around the distinction between how-possibly explanations and why-necessary explanations. Rosenberg provides a particularly nice accounting of the role of how-possibly explanation occupies in his view of developmental biology:

> there is an important asymmetry between how-possible and why-necessary explanations…. Once a how-possible explanation has been given, it makes perfect sense to go on and ask for a why-necessary explanation. But the reverse is not the case … a why-necessary explanation is more complete than a how-possible explanation, and that is the source of the asymmetry between them. (44)

Here, Rosenberg explicitly characterizes how-possibly explanations as inherently lacking explanatory completeness, while why-necessary explanations present immediately as complete.[2] Similar, though non-explicit, conceptions of how-possibly explanations are plausibly manifest

exhaustive metaphysical accounting of a targeted explanandum. But explanatory completeness here is much more humble. It simply presumes that there are paradigm explanations that are not wanting qua explanation (e.g., the striking of the match completely explains the match's lighting and the height of the flagpole completely explains the length of the shadow).

[2]Attentive readers will note that Rosenberg describes why-necessary explanations as "more" complete than how-possibly explanations. This is because a "complete" explanation for Rosenberg is extremely demanding metaphysically speaking, since it requires a full accounting of *all* causal factors. As revealed in footnote 1, I've set this issue aside for purposes of this essay, adopting a somewhat deflationary view of "complete" explanation.

in elements of Michael Weisberg's (2013) discussion of models as well as Carl Craver's (2010) account of mechanisms and mechanistic sketches. Cases like Rosenberg, Weisberg, and Craver show that the core element in Brandon's view of how-possibly explanations as incomplete is neither unique nor uncommon. But Brandon provides a concrete proposal for understanding *why* they are—at least in the evolutionary setting—incomplete, and for that reason I'll target Brandon's view of how-possibly explanations as a means of rejecting the view that they are inherently incomplete explanations.

Despite the *prima facie* success of Brandon's account in presenting how-possibly explanations as incomplete explanations, I want to suggest that there is some logical space for Dray's original position that how-possibly explanations are complete explanations. More precisely, I want to develop here a partial defense of Dray's original conception of how-possibly explanations as complete explanations—partial since Dray seemingly conceived all how-possibly explanations as complete. Accordingly, a preliminary point for my position is that 'how-possibly explanation' is not a univocal concept in my view—that, in fact, it admits of multiple interpretations. Indeed, I suspect that there may be quite a variety of ways to interpret the concept of how-possibly explanation; but my aim here is to distinguish between just two. The first, of course, is the Brandon-type interpretation, which, as outlined above, makes evident the incompleteness of those explanations. But in addition to the Brandon type interpretation, I contend that there is at least one other way to interpret how-possibly explanations, and under that interpretation how-possibly explanations are complete explanations.

Notably, the view that how-possibly explanations in biology do, at least sometimes, represent complete explanations is rare but not unprecedented. Patrick Forber (2010) has argued, for example, that certain instances of how-possibly explanations represent a distinct kind of explanation, and it is these how-possibly explanations that are complete. Briefly, Forber's analysis draws a distinction between what he calls global and local how-possibly explanations. This distinction is founded on whether a model explanation—in evolutionary biology in his case—is targeting concrete particulars in the world. A local how-possibly explanation references concrete particulars. A global how-possibly explanation, by contrast, is a model explanation that abstracts away from any particulars, offering a purely formal account of how a state of affairs might have obtained. Thus, a global how-possibly explanation will set out as a component of an evolutionary model an abstract variable for a population of organisms rather than some particular population with its actual features (e.g., its size). These global how-possibly explanations, in turn, define the constraints by which some state of affairs could possibly obtain. Moreover, these global how-possibly explanations are complete, since the objective in constructing these models is to demonstrate that a targeted explanandum (e.g., the frequency of some allele in a population) can be actualized by the parameters set out by the model. As Forber summarizes it, the models "need only show that some outcome or pattern is consistent with a specific set of information" (39); thus, relative to their goal, the explanations provided by global formal models are complete.

Forber's view of how-possibly explanations is in important ways a sensible extension of Dray's original conception. Foundationally, Forber, like Dray, seeks to characterize how-possibly explanations as a distinct type of explanation. Brandon's view, recall, implicates the incompleteness of how-possibly explanation in their being measured by degree of evidential support, though this holds for cases involving an incomplete set of explanatory factors as well. Additionally, that type distinctiveness is a significant element to demonstrating that how-possibly explanations are complete explanations. Indeed, if how-possibly explanations do represent a distinct type, then the criteria for assessing their completeness is type-relative. This I take as manifest in the above quote from Forber and is emphasized throughout Dray's original charac-

terization of how-possibly explanation.

Despite the appeal of these foundational elements, it is not evident that Forber's approach is fully satisfactory. One source for concern is the lack of generality that Forber's account has for how-possibly explanations within biology. As indicated previously, David Resnik (1991) successfully shows that how-possibly explanations are pervasive throughout biology. Forber's view would entail that only a fraction have the status of complete explanations. Of course, Forber might be correct that only a fraction of how-possibly explanations in biology count as complete; the rest, he may maintain, simply fit with Brandon type thinking that they are incomplete explanations. My view, however, is that Forber's account of how-possibly explanations is too restrictive, mistakenly narrowing complete how-possibly explanations to those given by certain formal models. I contend, by contrast, that an alternative approach to understanding complete how-possibly explanations can be extended to other areas of biology.

One way to begin to develop a more expansive alternative to Forber's restrictive view is to return to core elements in Dray's original characterization of how-possibly explanations. Dray summarizes his characterization of how-possibly explanations by stating that in some cases "explanation is called for because what happened seemed impossible" and the goal of such explanations is to "rebut the presumption that it could not have happened" (160–161). Forber sensibly deviates from Dray on some of the details surrounding the probabilistic/modal elements of Dray's characterization. Furthermore, Dray attempted to establish the type distinctiveness of how-possibly explanations quite differently than does Forber. For Forber, the type distinctiveness of how-possibly explanations appears to depend primarily on the instrument of explanation, namely formal models. For Dray, the type distinctiveness of how-possibly explanations focuses more on explanatory context.

My view is that Dray is correct to source the distinctiveness of how-possibly explanations in the explanatory contexts in which those explanations appear. The key element in Dray's position on how-possibly explanation is expressed by his point that "The two kinds [why necessary explanation and how-possibly explanation] … are logically independent in the sense that they have different tasks to perform. They are answers to different kinds of questions" (162). Dray then focuses on the last sentence of this selection, seeking to solidify this point by driving a sharp conceptual wedge between how questions and why questions. Contrary to Dray, I do not believe that the type distinctiveness of how-possibly explanations is gained by appeal to the difference between how questions and why questions. Indeed, what I seek to demonstrate is that it's not just the particular question, but a more extensive conception of explanatory context, that secures their distinctiveness.

The idea of explanatory context, I argue, is inclusive of not only the type of question that is posed but also of matters such as the expectations and demands of the audience of an explanation, as well as the terms permitted and prohibited in the explanation. It is explanatory context that is the key to understanding the way in which how-possibly explanations can serve as complete explanations.

Start with a broad outline of the two explanatory contexts. The first explanatory context poses a why question that seeks an inventory of factors, as well as the evidence for those factors, that are sufficient (together with background assumptions) to account for the targeted explanandum (i.e., a set of factors that we would justifiably allow us to expect some state of affairs to obtain). The second of the explanatory contexts, by contrast, poses a why question as to whether a particular *explanatory strategy* is appropriate for explaining a targeted explanandum. Let's call the first of these explanatory contexts the "sufficiency context" and the second the "strategy context."

The sufficiency context has been the dominant concern in philosophical analysis of expla-

nation. The traditional focus on laws, causes, and mechanisms in discussions of scientific explanation has been based on an interest in providing an analysis of what properly accounts for the height of a flagpole, the frequency of an allele in a population, episodic memory, etc. The strategy context, however, has not to my knowledge been focus. Nevertheless, I think the strategy context is a routine part of biological practice, if not scientific practice generally. Even more, the strategy context is crucial to understanding the full nature and role of how-possibly explanations.

At the center of the strategy context is the notion of an explanatory strategy. A strategy is a general approach for achieving some practical aim. Strategies set out the terms, resources, and constraints that one will use in attempting to achieve some end. Strategies, moreover, can be abstracted away from any particular implementation of them; they lie, that is, at a higher level of abstraction relative to their instantiations. Consequently, strategies are also distinguishable from any particular implementation of them with respect to matters of evaluation. One may fail to achieve some end by executing a particular course of action, while still recognizing that the strategy adopted was appropriate for achieving the end.

In order to further clarify the points about strategies offered above, consider briefly an illustration focused on investment strategies. Different investment strategies will make use of different resources—stocks and bonds, for example. These different strategies will also outline the guidelines for executing the strategy: the level of required tolerance for volatility and risk of financial loss, for instance. Furthermore, the appropriateness of using some investment strategy, given one's aims, can be evaluated quite separately from whether the particular implementation of the investment strategy led to one actually achieving the objective.

Suppose I adopt as my objective, and my only objective, achieving the maximal value for my retirement fund while also having a high tolerance for volatility and financial loss (but holding constant such things as income and contributions). I should, therefore, adopt an aggressive investment strategy, in order to optimize my chances for higher returns. But once I adopt the aggressive investment strategy, I will also need to execute that strategy by selecting some particular suite of investments. Furthermore, the particular suite of investments I select may fail to maximize my retirement nest egg (e.g., a different suite of investments may well have provided me a bigger retirement nest egg). Nevertheless, the failure to achieve my aim of maximizing my retirement nest egg is no indictment of my committing to the aggressive investment strategy. Indeed, the aggressive investment strategy is the best general approach to maximize one's retirement nest egg, even if the implementation of that strategy fails to lead to the desired end.

The above example does much to illuminate the distinction between evaluating strategies and evaluating the implementation of those strategies. Yet that distinction does little to articulate the *explanatory capacity* of strategies, and it leaves unaddressed the terms for evaluating whether an explanatory strategy can help us understand the completeness of how-possibly explanations.

Turn first to the explanatory capacity of strategies. By extension from the above, an *explanatory* strategy is simply a general approach adopted for purposes of accounting for some state of affairs. An explanatory strategy will set out the terms, resources, and constraints for securing a specific instance of an explanation subsumed by an explanatory strategy. One worry that is likely to arise at the outset concerns an apparent tension between strategies and explanation. Strategies, one may point out, set out the terms of explanation, but they don't themselves serve an explanatory role. They instead provide the means of explanation. The example of investment strategies might be thought to buttress the point. Naturally, investment strategies lay out potential courses of action. They are, in short, principles for decision-making. To the degree they operate at all in an explanatory capacity, they merely categorically subsume particular explanations. For example, a specific suite of investments can explain the size of my nest egg, but the

strategy simply categorizes that particular suite of investments. As sensible as this point first appears, I contend that it ultimately neglects to observe the nuanced ways in which strategies can explain.

Notably, the worry outlined above is similar to a critique Thomas Reydon (2012) levels against Forber's view. Reydon's critique of Forber is that abstract formal models cannot explain. The reason for this is that formal models are free of empirical content, and correspondingly, lack an identifiable explanandum. Purely formal models, therefore, do not explain any *thing*. Similarly, if an explanatory strategy is to prove explanatory, it must conform to the general criteria for explanation, which would include targeting identifiable phenomena. Importantly, though, the level of abstractness inherent in explanatory strategies is not such that it abstracts away from empirical content (e.g., the aggressive investment strategy targets the retirement fund's final value), which I take as a potential advantage of my account versus that of Forber's. Nevertheless, a critic might still persist that it remains unclear if strategies can explain, and, if they do, how they can be shown to explain.

One way of attempting to address the above issue is by following Michael Strevens (2011) in recognizing that what is at issue is an understanding of the "explanatory relation" between explanatory strategies and a targeted explanandum. It would, of course, be an understatement to point out that the substance of the explanatory relation is contentious. The success of an argument regarding how-possibly explanations' completeness should not, however, be contingent on resolving the overarching question about the nature of the explanatory relation—whether it is nomic regularity, causal, pattern subsumption, etc. Still, one might insist that, if the argument depends on an appeal to explanatory strategies being explanatory, it is essential that one demonstrate the explanatory capacity of these strategies by establishing a plausible fit with at least one of the contending accounts of the explanatory relation. Suppose, then, for the sake of evaluating the explanatory capacity of strategies, we adopt Strevens' own ecumenical difference-making account of explanation. The key question, then, is, can a strategy function as a difference-maker in an attempt to account for some state of affairs? I maintain that it can.

Return now to the example of investment strategies. Suppose my retirement nest egg has some value x. An explanatory project can certainly be initiated by asking, Why did the value of my retirement nest egg reach value x? Or even more precisely, Why does my retirement nest egg have value x rather than y (where $x > y$)? Now, a proper understanding of explanation in this case demands attending first to the explanatory context. The default interpretation is to see an explanatory project as set within the sufficiency context. The sufficiency context, in turn, circumscribes not only the particular question asked, but also the expectations of the audience to the explanations and the appropriate terms available for explanation. Within the sufficiency context, the most straightforward instance of a complete explanation is the actual suite of investments that were selected. Additionally, there is a how-possibly explanation that is an incomplete answer to the same question, again within the sufficiency context. In that case, what is provided is an inclusion of only some (the partial list of *known*) investments that led to the retirement account's value. In addition to these two explanations, however, I maintain there is also a how-possibly explanation that is set within the strategy context.

The strategy context shifts the availability of explanatory terms from an inventory of specific factors instantiating a strategy to just the strategy. The concern, however, is that identification of just a strategy makes an actual explanation impossible. But the example of explaining the value x of the retirement fund demonstrates that this is a mistake. To be sure, a strategy will be explanatory only if the context allows strategies as a type of thing that can explain, that is, if the audience allows for, and can expect, a strategy as an explanatory factor. But the question whether a strategy can actually be explanatory turns on whether the strategy cited is a difference-

maker for the targeted explanandum. The investments example demonstrates that it can. The identification of *the aggressive investment strategy*, quite independent of the particular suite of investments constituting that strategy, can explain the value of the fund. Indeed, if we suppose there is a set of all available investment strategies, and only the aggressive strategy is consistent with the retirement fund having the value that it does, then the aggressive investment strategy is a difference-maker, for had the strategy been different, the ending value of the retirement account would also have been different.[3] The strategy, therefore, is a difference-maker and, thus, explanatory.

The above, I hope, clarifies the explanatory capacity of strategies; but that is only one further step to showing that how-possibly explanations offered within the strategy context can be complete explanations. The additional component necessary to secure the explanatory completeness of how-possibly explanations turns on a feature about the audience to the explanation. Recall that Dray characterized one crucial feature of how-possibly explanations as "efforts to rebut the presumption that a state of affairs is impossible." Forber rightly worries that this characterization of how-possibly explanations invites problems. A principal worry is that a formal interpretation of 'impossible' would prohibit any revision, through Bayesian updating, to the formal measure of possibility for the explanandum.

One way to formulate better the feature that Dray seeks is to force a conceptual shift away from the impossibility of states of affairs and toward a feature or features about the audience to how-possibly explanations. Sensibly, these two considerations were tied together in Dray's thinking, but that need not be the case; one can construct a non-probabilistic formulation of audience demands and expectations suitable for thinking about how-possibly explanations. Indeed, let us say that a how-possibly explanation offered within the strategy context has as a necessary condition that the audience to how-possibly explanation adopts *an attitude of incredulity* regarding some state of affairs. This alternative characterization psychologizes the task set for how-possibly explanations. The task is to meet the challenge set by audience attitudes rather than overcome a mathematical representation of a metaphysical matter. To be sure, an attitude of incredulity might be assigned a mathematical measure; but nothing in 'incredulity' implies a zero, rather than just very low, probability measure. Most importantly, this attitude of incredulity can be defeated by identifying an explanatory strategy that accounts for the explanandum (i.e., that is a difference-maker for it).

As an important aside, the above account has an unmistakable subjectivist character to it (e.g., the *attitude* of incredulity). But it's essential to recognize that the account doesn't imply explanatory anarchism. The normal terms of successful explanation apply (e.g., empirical adequacy, internal consistency, etc.). In addition to those features, however, a complete how-possibly explanation within the strategy context requires an audience that, given their existing epistemic commitments is incredulous of the explanandum. But, in view of the strategy formulated to explain how-possibly that state of affairs arises, an earnest audience should reject their attitude of incredulity. Moreover, since this is the explanatory task set within the strategy context, the how-possibly explanation is a complete explanation. Alternatively, unlike the sufficiency context, the identification of the strategy as an explanation within the strategy context is not deficient qua explanation. Of course, the attitude of incredulity might also be defeated

[3]Note that I've set up the case with an idealizing supposition that the aggressive investment strategy is the only one consistent with the ending value of the fund to make the point as clear as possible. But this idealization shouldn't materially affect the general lesson. The explanandum—the value of the fund—is set, so even if there are multiple strategies consistent with the value, as long as there are some that aren't consistent, citing the aggressive strategy is a difference-maker. Similarly, a recognition that the aggressive investment strategy does not guarantee the fund having the value that it does doesn't affect its difference-making capacity. Again, the fund has the value that it does, and it has it, at the relevant level of abstraction, as a result of the strategy used.

by working within the sufficiency context, and within that context, providing either a complete inventory of factors to explain the state of affairs or an incomplete inventory of explanatory factors, this just as Rosenberg suggested in his discussion of how-possibly explanation. The point here, however, is to explicate an alternative in the form of the strategy context. In this context, the aim is to identify a successful explanatory strategy; and, within the strategy context, the identification of an appropriate strategy can completely explain by defeating the attitude of incredulity held by an earnest audience to the explanation.[4]

3 Wilhelm His's simple-experiments models as a Case Study in How-Possibly Explanation

In this second part of the essay, I aim to outline a historical case study which illustrates the account of how possibly explanations offered in the first part of the paper. The case study focuses on the research of nineteenth century German developmental biologist Wilhelm His (1831–1904).

Developmental biology in the nineteenth century was alive with rival theories about how animals develop from conception. The late nineteenth century, though, also marked a turn to a modern era of developmental biology. The turn is frequently traced to the work of Wilhelm Roux (1850–1924) and the so-called *Entwicklungsmechanik*: a broadly mechanistic approach to development that emphasized direct experimentation on, and corresponding material explanation of, developing organisms. Notably, though, Roux was preceded in this mechanistic framework for understanding animal development by the work of Wilhelm His.

His's importance to developmental biology's shift to a mechanical framework was gained through his novel means for the meticulous study of embryos. His, for example, developed the technique of the microtome, a technological advance that empowered the embryologist to slice embryos into histological sections. Arguably, though, His's most underappreciated accomplishment was his efforts at representation of human development through various models (Hopwood 1999). One dimension of His's modeling was an effort to carefully represent the sequential stages of development. This endeavor required acquisition of dozens of human fetuses aborted at various stages of development, but also the attentive work of artists' drawings, expert photography, and precision wax modeling. His commissioned wax models ultimately became widely available, and were a standard pedagogical instrument for embryology. This first recognizable dimension, then, of His's role in modeling development is purely descriptive; however, in addition to this descriptive aim, there was a second dimension to His's modeling that was explanatory in nature.

Despite the expanding perspective of a mechanical framework for understanding living systems, the mechanical analogues that helped illuminate physiology (e.g., fluids in pipes) were not yet available for the embryologist. Consequently, as Nick Hopwood (1999) admirably details, His was forced to envision and create for himself novel mechanical analogues that would serve to demonstrate the matter and force interactions capable of bringing about the changes observed in embryos over the course of their development (470–473). His turned to rather sim-

[4]There is one other complicating factor to this view of evaluating the success of how-possibly explanations: those how-possibly explanations that are knowingly counterfactually constructed, which is say they are known to be inconsistent with the facts. Michael Weisberg (2013), for example, discusses the case of a three-strand, genetic molecule. These cases may well deserve special attention, but I don't see them as presenting an immediate challenge to the terms of evaluation presented here. One could simply specify that *certain* epistemic commitments are suspended in these cases, but explanatory success would still be measured by consistency with those non-suspended epistemic commitments.

ple materials such as leather straps and rubber tubes, physically manipulating them in various ways that would mimic the characteristic transformations of developing embryos. Hopwood (1999) describes His's use of the rubber tube thusly:

> For example, [His] explained the development of the central nervous system by modeling it using a rubber tube with moderately elastic walls and a relatively wide bore. The characteristics spindle-shaped gaping of the developing medullary (neural) tube was just what one obtained by slitting a rubber tube along part of its length and applying a convex bend. More elaborately, His used the same rubber tube model to explain the formation, by folding perpendicular to the axis, of the major divisions of the brain. The most anterior fold was produced by longitudinal growth of the medullary tube while it was attached to the foregut; this could be imitated exactly by pulling back the open end of a rubber tube with a twill thread. (471)

As an overarching point, it should be evident that, unlike His's drawings, photographs, and wax models, these simple-experiments models were pursued for explanatory purposes. But just what explanatory role they occupy is not obvious.

One of the reasons I take His's simple-experiments models as an ideal case study for examining how-possibly explanations centers on the inevitable temptation to presume that their explanatory value is measured within the sufficiency context. The idea here is simple. On examining His's mechanistic view of development, made manifest in the simple-experiments models, the proponent of the Brandon view of how-possibly explanation will immediately judge them as a foundation for a radically incomplete how-possibly explanation of animal development. And, as Resnik would describe matters, His provided an explanation that operates as heuristic for the continued study of animal development. But I think further scrutiny of His's life and work casts serious doubt on this account of their explanatory value. Indeed, there is a near implausibility in understanding His's simple-experiments models as attempts to provide even an abridged inventory of any actual causal-mechanistic factors that determine animal development. Notice that it is His's *hands* that are the underlying causal factors transitioning a leather strap, for example, from a flattened state to a tubular state. His's hands push, pull, pinch, and squeeze the physical substrates that he uses, and yet, human hands are obviously not the causal-mechanistic factors responsible for the transition of the relatively flattened back of a chordate to a tubular state. The implication in recognizing this basic fact is that His's simple-experiments models ought not be understood as an explanatory project set within the sufficiency context. The models simply do not establish any of the inventory of developmental factors that actually bring about development.[5]

But if not the sufficiency context, then this question remains: Is it sensible to interpret His's research as being carried out within the strategy context? I contend it is, but an appreciation for why that is demands attending to the historical setting in which His pursued his simple-experiments models. My aim, I want to emphasize, in surveying the historical setting in which His carried out his research is not an attempt to interpret precisely His's own thinking, but rather to use the historical period in a way that illuminates the strategy context of how-possibly explanation.

At the time His began pursuit of his simple-experiments models, developmental biology lacked a governing paradigm. Vitalism, for example, persisted as a framework for thinking about development, gaining prominent supporters even at the turn of the century (e.g., Hans

[5]The best case that might be made for the sufficiency context is to identify the factors as "physical matter and forces," but that is so weak a characterization of the factors as to make the position effectively vacuous in the sufficiency context, and indeed, ultimately is just a veiled characterization of the explanatory strategy.

Driesch). But for His, it was the influence of Ernst Haeckel's evolution-based theory of development that posed the greatest obstacle to the advancement of understanding development. Haeckel's biogenetic law described the successive stages of development as a process of recapitulation of evolutionary history. According to Haeckel, a developing organism would successively transition from an ancestral form to a descendent form, culminating in its ultimate form, and each of these stages of development would be a manifestation of an evolutionary ancestor of the developing organism. Haeckel's theory has a strong teleological character to it, since an organism is, in some sense, predetermined to develop as it does in accordance with the biogenetic law.

As an early mechanist with respect to explaining animal development, His viewed Haeckel's theory of development as deeply misguided. In fact, it is near impossible to overestimate just how distinct His's and Haeckel's respective approaches to understanding development were, a point reinforced by the distaste that both men ultimately felt and revealed for the other. The most recognized episode illustrating the intellectual divide that separated Haeckel and His came when His attempted to expose Haeckel's now famous drawings of embryological recapitulation as distorted representations of actual embryos. But a narrow focus on just this episode obscures the broader narrative that helps illuminate the explanatory role of His's simple experiment models.

His's interest in chastising Haeckel for his drawings was part of a wider effort to standardize the handling and depiction of embryos at distinct stages of development (Hopwood 2000). But His did specifically target Haeckel for advocating his recapitulation theory. Haeckel introduced his biogenetic law in 1866 with the publication of *General Morphology of the Organisms*. In 1869, His delivered a lecture at the University of Basel in which he laments the trend to understand development by way of phylogeny, this following his 1868 publication of *Researches into the Earliest Form of the Vertebrate Body* where he advocates for the causal-mechanical approach to embryology. In 1874, Haeckel produces *The Evolution of Man*, in which he directly responds to His and his 1868 publication by deriding it as "seriously marred by ignorance of comparative anatomy," and more salient for purposes here, states that mechanical principles "are of no value" in explaining embryological phenomena (19). But 1874 also sees His publish *Our Body-Form and the Problem of its Development* where he details his simple experiment models. This somewhat circumspect historical sketch is strongly suggestive that the simple-experiment models were a culminating effort, and that they were integral not only to advancing the causal-mechanical approach in embryology generally, but, perhaps even more so, to rebutting Haeckel's past, as well as on-going, opposition to His and his explanatory approach. This historical sketch can be used to illustrate the role how-possibly explanation occupies in the strategy context.

Those who insist His's building of the simple-experiments models is an explanatory endeavor whose value is gauged within the sufficiency context are compelled to view His as *solely* attempting to construct the models as an answer to the "Why development?" question where the relevant contrast is "rather than no development." The how-possibly answer to that question requires citing a subset of those developmental factors that would partially contribute to animals developing rather than not developing. I argued above that this characterization of the explanatory value of His's simple experiments is not plausible even in the absence of any historical context. The historical context outlined above only furthers its implausibility; however, with that historical context in place, an alternative view emerges. His can be understood as answering the "Why development?" question, but the relevant contrast is "according to a mechanistic strategy rather than the phylogenetic strategy." Recognize that His's and Haeckel's respective views are taken by the other as incompatible with one another. That is, they are rival strategies. Indeed, there is little doubt that a primary motivation for Haeckel writing as he did

was that he had adopted an attitude of incredulity regarding mechanistic explanations of animal development. As part of the critique of His in *The Evolution of Man*, for example, Haeckel explicitly addresses His's claim of the "non-necessity" of phylogeny to embryological explanation, dismissing it out of hand (19–20). This I read as Haeckel believing that developmental explanations are impossible with only mechanical principles (i.e., neglecting phylogeny). Thus, when His constructs his simple-experiments models, he introduces an empirical demonstration that discredits the phylogenetic strategy. It does so by defeating the attitude of incredulity towards its main competitor, the mechanistic strategy.

This last point ushers in the key implication from the His case study, namely that we can view His as having offered a how-possibly explanation of development that is explanatorily complete. The completeness of His's how-possibly explanation of animal development depends first on observing that the relevant explanatory concern is between competing explanatory strategies. The second, and more crucial point, however, is that the completeness of His's how-possibly explanation is secured by achieving their aim: to defeat the attitude of incredulity toward the mechanistic explanation of animal development. This is done, again, by His showing that the simple-experiments models are an empirical representation of development carried out according to his favored explanatory strategy (i.e., the mechanistic strategy) but not its rival (i.e., the phylogenetic strategy). Once more, within the strategy context, the explanatory project is focused on defeating the attitude of incredulity held by an audience (i.e., Haeckel), this by identifying some explanatory strategy that is a difference-maker for the explanandum. His's simple-experiments models demonstrate that mechanical factors are difference-makers for animal development. That is to say, with the representational operation of various mechanical factors, we observe representational states and stages of animal development, though no such observation is made in the absence of those representational mechanical factors.

The case study of His's simple-experiments models does a great deal, I think, to support the view that some how-possibly explanations are, in their own way, complete explanations. But the case study is also likely to invite critical reactions.

One notable critical response that might be marshaled against this strategy-based defense of the explanatory completeness of how-possibly explanation focuses on whether the His case study is generalizable in a way that makes the view salient for biology as a whole. Recall that one issue with Forber's account of complete how-possibly explanations is that it is not obviously generalizable to the various sub-fields of biology, this despite the prevalence of how-possibly explanations in biology. The motivation for this objection is no less sensible for the strategy-based view I've offered here than it was for Forber's narrow evolutionary models view. In this case, His's explanatory contributions were introduced as an ideal illustration for the strategy account, since it focuses on radically distinct explanatory strategies. But it is not at all evident that sub-disciplines throughout the biological sciences reveal within them sufficiently distinct explanatory strategies necessary for the actualization of complete how-possibly explanations.

The crucial point for responding to this objection is to appreciate that the His case study is certainly an ideal but it is not thereby less representative of a common feature of biological explanation, namely that competing explanatory strategies are routine in biology. One way to gain an appreciation for this point is to examine other case studies of how-possibly explanation that claim to establish their incompleteness, assessing whether the strategy based approach used to understand His's explanatory project fits with these other case studies.

Consider, then, Alisa Bokulich's (2014) examination of the different models, formulated at different levels of organization and informed by different degrees of empirical information, that are used to explain the banding patterns in tiger bush. Bokulich states that her analysis of the case loosely fits with Brandon's view of how-possibly explanation, but rejects that view's neglect

of explanatory context as well as its measuring of completeness along a single continuum regarding empirical information. Bokulich explains that models, as illustrated by those offered to explain tiger bush banding patterns, are constructed at different levels of abstraction. Moreover, a model, she contends, at higher levels of abstraction can serve as a how-actually explanation, while models populated with greater detail, and are informed with more empirical content, may provide only how-possibly explanations.

Bokulich's account of how-possibly explanation has important points of convergence with my own.[6] Her emphasis on the significance of explanatory context and levels of abstraction is in-line with the view I've offered here. But Bokulich, I contend, sets her analysis of how-possibly explanations exclusively within the sufficiency context, and thus misdiagnoses the way in which explanatory context and levels of abstraction impact the issue of how-possibly explanation's completeness.

As part of her analysis, Bokulich surveys a range of models that have been constructed for explaining tiger bush banding patterns observed across diverse types of vegetation and in distinct locations. As she explains, at a higher level of abstraction, researchers have drawn a contrast between "deterministic symmetry breaking instability" models and "stochastic noise-induced" models. And under each of these model types are the lower-level models that execute the respective abstract model types in particular ways. Bokulich explains that the majority of researchers into tiger bush patterning "seem convinced" that the deterministic model type is accurate. Additionally, if they are correct, this would make that model type a how actually explanation; however, the various lower-level models would still serve as how-possibly explanations, assuming none of them provides a full accounting of tiger bush banding patterns. What I want to suggest here is that even if this analysis is right along the how-possibly versus how actually dimension of the case, it neglects to appreciate the way in which how-possibly explanations represent complete explanations.

Bokulich initially identifies both the deterministic model type and the stochastic model type as how-possibly explanations. It is only under the supposition that the majority of researchers are correct about the deterministic model type that we are to consider it a how actually explanation. Imagine, however, we don't grant that supposition. Furthermore, let's interpret the point that the majority of researchers seem "convinced" of the deterministic model's accuracy as signaling their having an attitude of incredulity toward tiger bush banding patterns arising under any conditions not subsumed by the deterministic model type (by conditions specified by the stochastic model type, for example). Recognize too that under my view, the deterministic and stochastic model types represent explanatory strategies. That is to say, they are both general approaches to explaining a state of affairs, wherein each can be implemented in distinct ways. Now we consider again the stochastic model type presenting, just as Bokulich initially sets out, a successful how-possibly explanation. More specifically, suppose the stochastic model type is empirically adequate, internally consistent, and that it identifies a set of conditions that make rationally expectant the appearance of tiger bush banding patterns (i.e., this set of conditions jointly represents a difference-maker). Assuming further, as would appear evident, that the deterministic and stochastic model types are incompatible, I maintain the success of the stochastic model type would compel us to recognize it as a complete explanation. Notice that this is *not* because it demonstrates the mechanisms by which tiger bush banding patterns in fact form, as the sufficiency context demands and Bokulich emphasizes. Rather, it is explanatorily complete because it satisfies its context-defined objective, namely to demonstrate a distinct means, believed non-credible by proponents of the deterministic model, of explaining how tiger bush

[6] An anonymous referee helpfully pointed out that Michael Cuffaro's (2015) account of how-possibly explanations in quantum computing also has similarities to my strategies account.

banding patterns could arise.

Once one begins to appreciate how Bokulich's tiger bush case fits the strategy-based account of how-possibly explanation, it should be easier to conceive of the potential for generalizing the account across biology. Models, of course, are both a powerful and pervasive tool within in biology, and Bokulich's insightful discussion of models' higher level of abstraction conforms neatly with my notion of explanatory strategies. The primary case study, then, of His and his simple-experiments models, is certainly an ideal illustration of explanatory strategies, but ultimately there is nothing unique about that case as it relates to how-possibly explanations operating in the strategy context.

4 Conclusion

A common view of how-possibly explanations treats them as explanatorily incomplete. There is, moreover, an important sense in which this view captures explanatory practice in biology. But in addition to this interpretation I have argued that there is another interpretation of how-possibly explanations, one which features explanatory strategies. This strategy-centered interpretation of how-possibly explanation centers on there being a different explanatory context within which how-possibly explanations are offered. In conditions where this strategy context is recognized and appreciated, how-possibly explanations can indeed be understood as complete explanations.

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