

EXPLORING BIOLOGICAL AGENCY AND EMBODIMENT TO
OVERCOME THE LIMITATIONS OF GENE-CENTRIC
PERSPECTIVES AND RELATIONALIZE BIOLOGICAL
SCIENTIFIC INQUIRY

by

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Exploring Biological Agency and Embodiment to Overcome the Limitations of Gene-Centric
Perspectives and Relationalize Biological Inquiry

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Much of 20th-century biology has been driven by and proceeded through a finer understanding of biological mechanisms at the level of genes and molecules. These gene-centric approaches have located medical interventions, clarified evolutionary histories, and identified molecular signaling pathways, among other invaluable contributions, by mechanistically decomposing biological systems into genetic parts to examine how their structure and functioning explain the system as a whole. However, biology and philosophy of biology scholarship reveal that studying organisms in terms of their genes is limited because it overemphasizes genetic components' role in development, inheritance, and evolutionary innovation and, in doing so, reduces organisms to the objects of their genes' predeterminations. Engaging biological case studies and philosophy of biology, I reveal that gene-centrism's limitations suggest the need for a complementary approach—biological agency—capable of recognizing organisms as agents of their genes, instead of passive objects of their genes' expression. Through this exploration, I show that a biological agency perspective realizes the ways in which gene expression is interactively shaped by organisms' spontaneous engagement with their environments, which is further indicative of organisms' context sensitivity and relational responsiveness. The biological agency approach overcomes gene-centrism's

limitations because it considers organisms as embedded in many intersecting and co-constitutive relationships—genetic, biological, and environmental—of which the organism responds to and accommodates into itself. Using perspectives from feminist epistemology and science studies, I question further into biological agency's account of organismal relationality to reveal that relationality does not just apply to the organism being studied, but to scientists as well.

Considering this extra dimension of relationality helps soften the boundary between subject and object and illuminates that biological scientific inquiry is performed by embodied researchers, theorizing is situated, and objectivity is subjectivity-dependent. Through this consideration, I hope to convey the viability of biological agency as a complement to gene-centrism and build appreciation for biological inquiry that not only recognizes organismal relationality, but the scientist's relationality.

Acknowledgements

In the preface of his book *Organisms, Agency, and Evolution*, Denis Walsh writes, “The old proverb says it takes a village to write a book” (xiii). My thesis is surely not a book, but the quote still holds. This labor of love I am calling a thesis surely wouldn’t have been possible without a village of support. I first want to thank my family—Dad, for the silliness to keep me lighthearted; Mom, for all the calls to help me organize my ideas; Daniel, for your silliness, too, and for listening to me talk to Mom and Dad about this thesis for the past year. Thank you, Casper, for holding my hand through this entire process, for your patience, gentleness, and solidarity. Thank you, Amanda, Laurel, and Drew. This thesis would not have been possible without my mentors and advisors—Barbara Muraca, Hope Healey, Bill Cresko, Carol Stabile, Nicolae Morar—who challenged, supported, and guided me through my first project of this size, in a field I knew little about when I first started. If there’s anything I’ve learned from this process, it’s that I have a lot of people to be grateful for.

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Introduction

The first tendrils of inspiration for my thesis grew out of unexpected places, many of which felt disparate and unrelated until other linking pieces fell into place¹ that could help pull them together. The first seed germinated in the fall of my junior year, in Chapman Hall, in an Evolutionary Biology class. We were tasked with reading excerpts from Richard Dawkins's *The Selfish Gene* as an introduction to the concept of evolution. It was early fall, still warm enough to sit outside, so I went to my favorite benches under the Douglas fir trees to do the reading. I say this because I don't typically remember where I am sitting when I complete readings for class, but these excerpts from *The Selfish Gene* must've been so memorable that their effect extended to my memory of my physical surroundings. Sitting there, I remember reading the opening sentence, "We are survival machines—robot vehicles blindly programmed to preserve the selfish molecules known as genes" (Dawkins 1976, xxi). This was the sentence that launched my thesis, or at least what it would eventually become. I recently went back to my copy of the text to find this sentence highlighted; next to it in the margin, I found an annotation that wrote, "I think there's something missing here...?"

I was aware that we were reading passages from *The Selfish Gene* as an introduction to evolutionary biology, that it was probably intended to serve as a conceptual setting-the-stage and not necessarily represent the actual 'meat and potatoes' of evolutionary biology or depict how practicing evolutionary biologists think about evolution, but there is something to be said for the

¹ Although I say, "fell into place," it usually was not this simple. Sometimes I would have the good luck of stumbling upon a scholar's work whose ideas bridged the ideas my argument was trying to make, but usually this was the product of hours of research, reading, re-reading, verbal processing with anyone willing to listen, advisor meetings, emails to professors I'd never met from universities I do not attend, and calls on the phone with my mom—which frequently happened once I reached points of what felt like madness, the tip-of-your-tongue feeling of being so close to it all making sense but knowing the logic of the idea is still not quite there.

fact we were reading the book in the first place. Indeed, the professor who assigned this reading is a practicing biologist who co-runs a population genetics lab and he thought it was relevant to include in his syllabus. As I was beginning to draft my thesis, I felt like it was necessary to cite Dawkins's perspective on evolution to establish the Modern Synthesis paradigm. I was and am certainly aware that Dawkins's perspective on evolution is a crude one, a caricature of the Modern Synthesis; I was hesitant to cite him out of worry that I would be isolating or making assumptions about audience members' understanding of evolution, particularly practicing evolutionary biologists and specifically Hope and Bill, my two advisors who actually *do* evolutionary biology and know more about it than I ever will. I respect their work immensely and I struggled to reconcile this with my knowing that, in my thesis, I would be critically exploring one of their fields of expertise as someone who just began learning about it. But as I began to identify and read other sources, I was comforted upon finding that many biologists and philosophers of biology and science whose scholarship I read, was inspired by, and engaged extensively throughout my thesis process—such as Walsh, Levins, Lewontin, Sultan, Anderson, and Keller, to name but a few—also found it necessary to quote Dawkins in their work, whether to establish a paradigm in evolutionary biology, mount a critique, or a combination of these things. Through further engagement with literature from feminist epistemology, feminist science studies, and decolonial sciences, I began to learn more about the oftentimes elusive intersection between paradigm and practice; Dawkins's reductionist and genetic determinist perspective may not seem to come into play in the everyday lives of practicing biologists, but it is indicative of a larger moment in Western science that shapes and is recreated in how we learn about and practice biology, as was certainly the case for me and my Evolutionary Biology classmates.

Though Dawkins neither trained in nor practices evolutionary biology, he certainly speaks loudly about it, as demonstrated by his popularization of the gene as evolution's primary unit of selection and his ability to reach general audiences and inform perceptions of evolutionary biology. While practicing evolutionary biologists' perceptions of the field might not be as directly susceptible to Dawkins's account of evolution, the fact that his voice reaches general audiences, reverberating through classrooms like mine and reaching the ears of voters and then to politicians, can have significant indirect effects that echo into the labs of practicing evolutionary biologists by shaping funding priorities, for example. Additionally, while Dawkins's representation of evolutionary biology is a fictionalized and highly exaggerated and does not literally depict the actual practice of evolutionary biology, there is a flicker of truth about the nature of twentieth-century evolutionary theory buried beneath his polemics that made them so appealing in the first place—figuring it out what this was fueled my exploration into other gene-centric² accounts of organismal life.

Dawkins's perspective was my jumping off point, my wake-up call to the paradigm of reductionism, gene-centrism, mechanism, and genetic determinism in biology. It started with Dawkins, who offers a very blatant window into gene-centrism, but upon more investigation into biology and philosophy of biology literature and personal reflection on my experiences in science classes, I noticed that gene-centric motifs are much more prevalent than I even realized. Returning to my copy of *The Selfish Gene*'s account of organisms and evolution to find the

² I more specifically define and delve into the features of gene-centrism in Section 2.2. In this context, I am using *gene-centrism* broadly to refer to biological approaches that emphasize studying an organism's genetic elements as a means to understanding organisms and organismal processes (e.g., evolution, inheritance, development). These approaches that embrace an organism's genetic elements as a lens through which to understanding some part of the organism are what I refer to as "gene-centric" methods.

annotation “I think there’s something missing here...?” is where my thesis began—what *is* missing from Dawkins’s perspective—and, by extension, other gene-centric, deterministic and mechanistic accounts of organismal life—and how might these potential limitations of such an account of organismal life manifest paradigmatically and practically, in how we learn about and are influenced by science and how we do science?

Section 1

1.1 Setting the stage

Denis Walsh opens his book *Organisms, Agency, and Evolution* describing his first time taking an ethology³ course, where he learned to make an ethogram. An ethogram is a record of the behaviors, movements, postures, and sounds exhibited by a specific animal of study (Walsh 2015). The ethogram is intended to serve as a tool to observe the manifestations of the animal's behavior without considering purpose or intention that might be motivating the behavior (Walsh 2015). For Walsh, this meant that the Columbian Ground Squirrels he was studying were standing on their hind legs at their full height, instead of looking out at the area for predators, or letting out a high-pitched 'bark,' instead of warning colony members of potential dangers (Walsh 2015). Walsh describes "dutifully" going along with the ethogram activity, despite observing that the squirrels were clearly looking for something. I felt a similar dissonance as I observed a mallard to make an ethogram for an undergraduate ecology course. While my ethogram comprehensively cataloged the mallard's behaviors, I couldn't help but think that surely the mallard's tendency to dunk her head into the pond or preen her wings was done completely without purpose.

While ethograms are meant to exclude purpose or intention from the observation of behavior, I came away from my ethological mallard-observing feeling conflicted and confused as to why it had such an aversion to purpose. I've spent hours poring over the pages of *Organisms, Agency, and Evolution*, but I always find myself coming back to this section of the book because

³ The scientific study of animal behavior.

it reminds me that Walsh also started out as an undergraduate student studying biology who felt like something was missing with the way he learned about organisms.

Walsh's ethogram anecdote serves to identify a recurring motif that is woven into the entire history of biology. There is tension within biology between the idea that organisms are natural entities to be studied like nonliving phenomena (unificationism), and that organisms are fundamentally unlike nonliving phenomena and should therefore be studied in such a way that acknowledges this distinctiveness (biological exceptionalism) (Walsh 2015). Strategies that have been employed and reemployed throughout the history of biology attempt to resolve this tension by de-emphasizing the aspects of organisms that set them apart from nonliving entities, relegating organisms' distinctive qualities to an incidental category, and positing that the principles used to account for nonliving phenomena are applicable to and adequate to explain living phenomena (Walsh 2015).

In many ways, these moves have been fruitful, and it would be entirely wrong to go on without acknowledging this. Indeed, much of twentieth century evolutionary biology—as well as many of biology's subdisciplines—has been driven by and proceeded through a finer understanding of biological mechanisms at the level of genes and molecules, which has circumvented the 'organism issue' by studying the organism in terms of its genetics (Walsh 2015). This has been productive in many ways; it has furthered scientific knowledge of molecular signaling pathways, identified genetic variants involved in disease which helps locate medical interventions, progressed genetic engineering technology, and clarified phylogenetic relationships and histories (Sultan et al. 2021). Focusing on genes and molecules dodges the organism issue because it enables the scientist to reorganize their study around the genetic

components of interest, which de-emphasizes the organism by explaining its activities through the lens of its genetic parts.

Circumventing the question of the organism's distinctiveness is epitomized by the Modern Synthesis of evolutionary theory, which rose to prominence during the twentieth century (Walsh 2015). The Modern Synthesis, as the name suggests, is a synthesis of ideas: on one hand Darwin's ideas of natural selection—which suggested a mechanism for the evolution of form and function—as well as his theory of descent with modification, and, on the other, Mendelian genetics. Darwin defined evolution as “descent with modification,” which was the notion that species change over time (Penny 2011). Evolution's mechanism, for Darwin, was natural selection: organisms with the traits best fit to survive and reproduce will tend to produce more offspring than organisms with less favorable traits, leading the more favorable traits to increase in frequency across generations. The Modern Synthesis theory of evolution merged Darwin's idea of natural selection with Mendelian genetics, creating population genetics (Millstein 2022). Uniting Darwin's ideas regarding evolutionary processes with Mendel's newly rediscovered laws of heredity was pivotal because it clarified that the mechanism of inheritance is genetic (Laland et al. 2015). This synthesis put evolution into a molecular, mathematical, and genetic context, as it yielded the popular understanding of evolution as the change in the genetic composition in a population over time (Gilbert 2000).

Evolution in the era of the Modern Synthesis is a genetic phenomenon concerned with the dynamics of genes—most simply known as a pieces of DNA that carry information to help determine traits. Evolution is commonly defined as the change in the genetic composition of populations (Chen et al. 2019); in order for evolution to occur, there must be changes in genetic variability and allele frequencies over time (Walsh 2015). Accordingly, the Modern Synthesis

theory of evolution takes the gene as its canonical unit of biological organization (Walsh 2015). Centering evolution around genetic changes enables the Modern Synthesis to avoid addressing the issue as to whether organisms and their processes are or are not distinctive from material entities by focusing instead on the dynamics of populations full of “information-encoding, suborganismal entities” known as genes (Walsh 2015, 80). Since the explanation of evolutionary phenomena in the framework of the Modern Synthesis primarily deals in terms of populations and genes, the organism itself and its properties that *cannot* be accounted for at the population- or gene-level are excluded from this account of evolution (Walsh 2015).

Surely, there are biologists inquiring into processes at the organism-level, but they tend to be less represented than population and molecular geneticists. For example, organismal biology is a field that connects the suborganismal realms of living systems (molecular, genetic, biochemical) with the supra-organismal scales of ecology and evolution (“Organismal Biology Research,” *Oregon State University*). However, “organismal biology” as a keyword search only yields 15,283 results on *PubMed* and 27,093 results on *Web of Science*, whereas “population genetics” and “molecular genetics” yields 339,129 and 1,995,809 results, respectively, on *PubMed* and 131,914 and 222,561 results, respectively, on *Web of Science*. I recognize that the disproportionate representation of molecular and population genetics publications from this example is not necessarily a reflection of individual scientists’ personal decisions to commit to research that de-emphasizes the organism itself. Rather, these trends are meant to represent the systematic commitment to the gene-centric logic popularized by the Modern Synthesis that is reinforced by structures like incentive and award opportunities that may be, and often are, topic-preferential.

I am not attempting to argue that the population and genetic accounts of evolution, as well as the spectrum of biological approaches that prioritize studying organisms as populations or in terms of their genes are wrong, “bad,” or unhelpful. Instead, I am arguing that these accounts of organisms have been incredibly productive in answering countless biological questions, but, like any framework, they have boundaries and limitations. These boundaries lie at the level of the organism itself, and the limitations can be addressed by embracing a complementary approach to the study of biology that emphasizes, as opposed to minimizes, the organism to account for its processes that cannot be completely addressed at the genetic and population-levels. Recent scholarship in philosophy of biology argues that this alternative approach is a *biological agency* perspective, which I will explore most in depth in Section 3.

Before delving into the limitations of gene-centric approaches to studying organisms and complementary approaches that can address these limitations, I turn to the history of biology to reconstruct the context shaping the gene-centric paradigm in Western scientific thought. I will focus on a few key developments in Western scientific thought and the scientists who brought them about to show how they contributed to de-emphasizing the organism and shifted the scientific paradigm towards a gene-centric study of organisms. It is important that this historical reconstruction include not only the scientific developments, but the scientists themselves because I want to highlight that scientific theories and frameworks always come from somewhere, from *someone*. Connecting scientific developments to the scientists themselves and their socio-historical position is valuable because it reveals that the theories we use to study organisms are not purely objective or neutral givens that materialize outside of social, cultural, and historical contexts. Rather, these theories and frameworks always come from somewhere and from someone(s) in a specific context. By connecting the science to the scientists in this

reconstruction, I intend to illuminate that the prominent gene-centric paradigm developed out of and was intimately informed by choices made by scientists whose work is socially formed and informed.

1.2 Feminist frameworks inspire telling the stories behind science

I am compelled to explore the history of biology as it led up to gene-centrism by reconstructing it in its socio-historical-political context to better understand how and why gene-centrism came about, and what assumptions about organisms it entails. Through this endeavor, I hope to elucidate the scientists along the way and the relationship between their socio-historical-political positionality and scientific work in order to reveal how their assumptions may have informed their theorizing about the study of organisms that may be implicit in the gene-centric study of life. I also intend to clarify the scientists and their scientific developments that helped in swinging the pendulum in the biological sciences away from a holistic study of organisms and towards one that is more mechanistic and deterministic.

My motivation for retelling this story about the rise of gene-centrism is inspired by voices speaking from the feminist epistemological tradition, namely Lorraine Code, Elizabeth Anderson, Donna Haraway, Martha Kenney, Sandra Harding, and Rosi Braidotti, as well as Patricia Hill Collins, Obioma Nnaemeka, and Sarojini Nadar, who speak specifically from the Black feminist tradition. Feminist epistemology reveals and raises questions about the situated nature of knowledge by illuminating the ways in which knowledge reflects assumptions, biases, perspectives and experiences of the knower.

1.2.1 Science is subject-related

Western science maintains a rhetoric of “objective purity” and “value-neutrality” by assuming that scientists are “standardized, faceless observers” who can “transcend the

particularities of experience” (Code 1996, 194) due to some presupposed universal or essential human nature that “allows knowers to be substitutable for one another” (Code 1996, 192). However, feminist epistemological discourse challenges the supposedly objective scientific realm by revealing that “evidence is *selected*, not found” (Code 1996, 205) and that scientific knowledge is not just a product, but a process guided by the observer’s values and their material, historical, cultural and political circumstances (Nadar 2014).

In order to take up this process of “objecting to objectivity,” feminist epistemology privileges subjectivity by attempting to relocate scientific inquiry as socio-political-historical activity (Code 1996; Nadar 2014). For example, in her essay “The Subject in Feminism,” Braidotti asserts that the primary site of analysis within the feminist framework is the body, which situates the subject as a “material embodied” entity, instead of an abstract one, allowing for the recognition of the body not as a natural thing but instead as a “culturally coded socialized entity” (Code 1996, 160). She then cites Gayatri Spivak’s (1987) point that “the embodied subject is neither an essence nor a biological destiny, but rather one’s primary location in the world, one’s situation in reality,” reiterating the emphasis on embodiment—“the situated nature of subjectivity”—in the feminist framework (Braidotti 1991, 160). Braidotti then shows that this framework enables the reconsideration of the “conceptual structures of biological sciences” by revealing the human subjectivity implicit in the “elaboration of systems of knowledge” (Braidotti 1991, 160).

Braidotti’s emphasis on the centrality of the embodied subject also reiterates Code’s point that “knowers are always *somewhere*” and therefore their theorizing will reflect and be influenced by their situation in the world (Code 1996, 213). This is not an inherently “bad”

thing,⁴ though numerous feminist scholars warn that it can be harmful when these “knowers” we know as scientists primarily come from socially privileged groups whose status informs and reinforces “social political structures of domination and submission” under the guise of objectivism (Code 1996, 198). Feminist epistemology’s emphasis on considering subjectivity is useful in this context because it can help expose the fact that science is subjectively informed, and the supposedly objective scientific realm is always imbued with cultural, social, and political assumptions that must be acknowledged. Following Harding’s (1995) concept of strong objectivity, recognizing scientists’ partiality does not threaten the objectivity of their science but strengthens it because it clarifies, instead of generalizes, the researchers’ positionality and partiality.

1.2.2 The story behind science

Clarifying that science is a subjective and socially informed practice is important because it reveals that the developments in biology towards the paradigm of gene-centrism are “socially and historically contingent, not the result of inevitable scientific progress” (Kenney 2019, 6-7). This is one of the reasons why it was important to me to spend time learning about and recounting how the gene-centric story about organisms came to be. In my science classes, I was neither taught where prevalent gene-centric theories, practices, and analogies came from, nor encouraged or given the tools to question them. As a result, (in my experience) science has been

⁴ Though her concept of “strong objectivity,” feminist epistemologist and standpoint theorist Sandra Harding (1995) points out that the scientist is not wrong or bad for being subjectively informed. Rather, she claims that objectivity is weakened or biased when the knower does not make clear their particular standpoint, as this also glazes over the fact that their position is not generalizable but particular. Harding proposes the idea of strong objectivity as a contrast to scientific objectivity in order to decouple neutrality and objectivity as assumed in scientific objectivity and reveal that the researcher’s biases and positionality inform their worldview and therefore their research as well.

shrouded in a cloak of validity and factuality due to its supposed objectivity and its detachment from social and historical contingencies. Science's guise of factuality and validity is also definitely not hurt by the fact that it receives disproportional funding at my university compared to humanities departments, for example, which certainly makes it appear much more serious and impressive to my peers, not to mention donors, than humanities fields.

In my humanities classes, more often than in my science classes, I learn about the socio-historical context that surround and may have influenced the texts I am reading. This can be clarifying and humanizing because it creates the opportunity to see how the texts are, in many ways, a reflection of and a window into the context of their creation. In my science courses, however, the theories I am learning about are rarely socially, politically, or historically contextualized, which positions the theories themselves as universal, context-dependent truths. Because of this, I am inspired to take up the project of exploring the stories behind science in order to understanding the metaphors behind the models, the surrounding paradigms and their relationship to scientific practice, and humanize and contextualize scientists themselves. Feminist science scholar Martha Kenney reminds us that we are responsible for paying "attention not only to what our stories say, but what our stories *do* as they move through social worlds" (Kenney 2019, 8). Recognizing that science is not exempt from this obligation is vital if we are to begin the process of re-embodiment our scientific practices and recognizing how this re-embodiment brings with it a moral and ethical dimension and therefore relations of responsibility that Western science attempts to obscure.

Stories come into being out of encounters, relationships, experiences that are historically contingent and specific to the place and relationships from which they emerge, though not limited to it in their scope. For example, "For feminist science studies scholars, the history of

science, technology, and medicine are inextricable from the histories of colonialism, imperialism, and warfare; scientific knowledge is part of the fabric that constitutes and transforms consequential categories like sex, gender, race, dis/ability, and sexuality” (Kenney 2019, 6). When we recognize science as story, we are given the opportunity to unveil the lineage of relationships to oppressive categories and histories from which it came and continue to inform, and that are immortalized through science’s ‘retelling.’ Repositioning science as a story, as I attempt to do in my historical reconstruction, further enables us to not only recognize these relationships, but “show that these developments are socially and historically contingent, not the result of inevitable scientific progress” (Kenney 2019, 6-7). Furthermore, in order to be remembered, stories must be passed down. Retelling a story is a deliberate act; similarly, if science is a story, then we are inclined to see its ‘progress’ as a deliberate passing-down—and therefore reiteration—of certain traditions, assumptions, and relationships, whether intentional or unintentional, as opposed to inevitable progress exempt from historical, social, and political contingencies.

1.3 Gene-centrism’s rise to prominence

In the following subsections of this section, and continuing into Section 2, I am inspired to highlight some of the individuals and their developments in the history of science and history of biology in order to take up Kenney’s project of repositioning science as story. While this story is situated within the broader context of my argument as it is largely built on a critical exploration of gene-centrism, it is not intended to criticize biology as a whole or the individuals who practice biology, or attack the figures whose work I choose to discuss in my exploration of the gene-centric paradigm. Rather, I am leveraging the implications associated with unveiling the story behind science and recognizing that science is subjectively informed in order to reveal the

overlap between the scientific and the social that has facilitated gene-centrism's rise to prominence.

I am beginning this exploration with Aristotle, as he is recognized as the originator of the Western scientific study of life (Lennox 2021). While there are certainly many ways to practice science that both overlap with and are distinct from Western science, this historical reconstruction begins with Aristotle, a Western thinker, because it explores the developments towards the gene-centric paradigm, which primarily descends from the Western scientific tradition. After briefly exploring Aristotle's notion of organisms in Subsection 1.4.1, Subsection 1.4.2 skips forwards to the sixtieth and seventieth centuries to Europe's Scientific Revolution because it marks a paradigm shift in the history of science towards the framework of logical empiricism and a mechanistic scientific methodology, as informed by breakthroughs in mathematics, as well as chemistry, astronomy, physics, and other physical sciences (Craver and Tabery 2019). This mechanistic methodology, primarily developed to aid in the study of physical phenomena, went on to inform biology, the study of life, providing many of its foundations, which I will argue were crucial in building towards the molecularization of biology and the "era of the genome" that characterize the twentieth and twenty-first centuries, respectively, and, more generally, the gene-centric paradigm (*National Human Genome Research Institute* 2012, quoted in Gannett 2008).

I want to preface this section by recognizing that it is told with the intention of reconstructing only *some* of the important developments that aided in the emergence of the gene-centric paradigm. I included individuals and figures whose work was most frequently highlighted by my mentors, in my classes, and in my selections of philosophy of biology literature as crucial in facilitating the gene-centric paradigm, but there are certainly many more important

developments and individuals I knowingly, and surely unknowingly, did not include. This was a choice on my part, because my intention in engaging in this scientific storytelling was not to account for all of the developments in Western science. Rather, my motivation for this storytelling is to begin practicing the feminist idea of reembodying science and implementing Kenney's idea of situating science as story into my own work by connecting science to scientists and exploring the ways in which scientific inquiry may be objective but never neutral⁵ because it is made up of choices made by individuals and groups alike as they are informed by a particular time and place. I also want to begin the following sections, and this section specifically, by reiterating that I am choosing to focus on the developments that facilitated and are indicative of a gene-centric paradigm in biology. I am aware that for every mechanist or genetic determinist in biology there was, and is, also a biologist or philosopher of science who chooses to explore organisms in the context of their environment or more holistically.^{6,7} I do not want to discount

⁵ When I say that science “may be objective but never neutral” I am pulling from Harding's (1995) idea of strong objectivity as a contrast to scientific objectivity to demonstrate that science may be objective in the sense of “strong objectivity,” but not neutral.

⁶ Organicist philosophy of biology, for example, emerged in Great Britain, Continental Europe, and the United States between the First and Second World Wars at a point in history when “the vast preponderance of active biological workers [were] mechanists” (Needham 1925, 235, quoted in Nicholson and Gawne 2015, 358). According to Nicholson and Gawne (2015), the organicists are unified in their beliefs that biology is distinct from physics and chemistry and therefore must be interpreted in the “context of the organismic organization that makes [it] possible” (367). Additionally, the organicists share in their understanding that organisms are distinctly unlike machines and therefore must be inquired into using theoretical tools tailored specifically to organisms (Nicholson and Gawne 2015). Finally, the organicists posited that biological organization is not only distinct, but that organisms themselves make up its central unit of organization and analysis (Nicholson and Gawne 2015). The organicists are one of many examples showing that there have always been scientists and philosophers in paradigms of gene-centrism and mechanism who advocate instead for studying the organism holistically and as a distinct entity with a unique form of organization compared to nonliving things.

⁷ It is also important to point out that while there are extreme genetic determinists who have rejected the role the environment plays in shaping organisms, there are also extreme cases of over-considering organisms' environments at the expense of all other factors. Soviet biologist, or, nominal biologist, Trofim Lysenko—“the Soviet era's deadliest scientist”—advocated for the

this fact but clarify that in Section 1 and the beginning of Section 2 I am intentionally focusing on the former because I am exploring the ideas that led to or are indicative of a moment in Western science when approaches that study organisms in terms of their genes are prominent.

1.3.1 Aristotle's organism had a soul

Reconstructing the story of the study of organisms as it has developed into the gene-centric paradigm requires going back long before scientists even knew about these things called genes. If genes, as a concept within biology, are meant to help tell a story about organisms and their processes, then the story of the gene is fundamentally a story about organisms and how they have been studied scientifically.

This brings us back to Aristotle, who is known today not only as a great philosopher, but also as the founder of the study of Western biology (Lennox 2021). Contrary to the pre-Socratic Atomists (such as Democritus and Empedocles) who believed that organisms are aggregates of atoms, Aristotle promoted the idea that organisms are distinct from non-living things because they possess a unique principle of organization which he refers to as a 'soul' (*psuche*) (Walsh

Marxist idea that the environment shapes organisms and exemplifies an extreme case of rejecting the role of genetics (Kean 2017). Having grown up incredibly poor at the turn of the twentieth century, Lysenko was an avid supporter of the communist revolution's ideals. He loathed the West and Western science and, specifically, the quickly developing field of genetics. Although the first Nobel Prize for genetics was awarded in 1933, Lysenko denied the concept of genes altogether as Western bourgeois bologna because they promoted the idea of fixed traits (Kean 2017). Taking the alternative extreme, Lysenko argued that the right environmental conditions alone drive plant and animal growth (Kean 2017). Stalin enlisted Lysenko to help "modernize" Soviet agriculture by creating and forcing farmers onto state-run farms operating according to Lysenko's backwards protocols (Kean 2017). Crop failure and famine ensued; at least seven million people died as a result of Lysenko's methods as forced into practice by Stalin, and an additional 30 million people died in Communist China where Lysenko's methods were also in practice (Kean 2017). While this example is certainly extreme, it serves to demonstrate that the over consideration of organisms' genes or their environment is flawed, and both must be appropriately taken into account.

2015). In *de Anima*, Aristotle's treatise on the nature of life and the mind, he argues that an organism's *psuche* is represented by its ability to organize around and pursue a specific goal depending on what type of organism it is:

Soul (*psuche*) is distinguished by a set of vital functions, nutrition, growth, locomotion and (in the case of humans) cognition. We may think of the form of an organism as a set of organizing principles, or a set of goal-directed dispositions, to organize its matter in such a way that the organism is capable of performing particular soul functions (in the particular way) distinctive of its kind. (Lennox 2001, 183, quoted in Walsh 2015, 5)

The organism's particular functions and activities are organized around and tuned to serve that specific organism's 'way of life,' or their distinctive purposes and goals (Lennox 2021; Walsh 2015). According to Aristotle, some regularities in the world happen because organisms pursue these purposes or goals. Therefore, if one seeks to understand an organism's behavior or structure, one can do so by employing teleological explanations that appeal to that organism's purposes (Walsh 2015). Walsh argues that Aristotle's depiction of organisms as beings that pursue purposes distinguishes organisms from nonliving entities that neither possess a soul nor organize around and pursue a unique way of life.

Contrary to Aristotle, the Atomists conceived of life as the result of random aggregations and mechanical encounters (Walsh 2015). Following this unificationist conception of life as indistinct from nonliving phenomena, the Atomists explained organisms by appealing to their parts to understand how they contribute to the organism's functioning (Walsh 2015). Aristotle, however, inverts the Atomist conception of organisms and juxtaposes unificationism through his argument that organisms and biological processes are uniquely unlike nonliving entities and physical processes. For example, *way of life*, for Aristotle, "explains the arrangement of parts and not the other way around" (Walsh 2015, 6). Instead of using the organism's parts to explain the

organism as a whole, Aristotle asserted that one can understand the organism's parts and structures by appealing to the purposes it pursues (Walsh 2015).

This exceptionalist/unificationist dialectic between Aristotle and the Atomists serves to demonstrate that the argument about the distinctiveness (or lack thereof) of life and how life should be scientifically accounted for runs deep in the history of science (Walsh 2015).

1.3.2 The Scientific Revolution's mechanical organism

Europe's Scientific Revolution marked a change in scientific thought, a shift away from biological exceptionalism and towards unificationism. Pioneered by scientists like Copernicus, Galileo, Descartes, Gassend, Boyle, Bacon, and Newton, the revolution was based on the belief that the natural world is like a machine. This paradigm shift is characterized by the methodology of mechanism and the understanding that the universe is nothing more and nothing less than matter in motion. Walsh (2015) points out that, as is often the case in science, the emphasis on mechanism in scientific thought solidified around a metaphor instead of a particular set of principles; in the case of the Scientific Revolution, this metaphor is the clock. The clockwork metaphor compares the natural world and the things inside of it to a mechanical clock. Therefore, understanding how and why things happen in the world simply requires taking them apart like one would a clock to investigate how the component gears work together to make the mechanism operate. René Descartes, a prominent French philosopher, scientist and mathematician during the Scientific Revolution, outlines this new conception of science in *Rules for the Direction of the Mind* where he asserts that science should proceed by breaking down complex phenomena into their simpler component parts. This method of reducing complex phenomena into constituent parts and reordering them in a controlled setting to see how they work together to pursue a

specific outcome that emerged during the Scientific Revolution is the ‘analytic method,’ and it is still the primary mode of investigation in science today (Walsh 2015).

While Aristotle promoted the notion that organisms possess souls and could be therefore understood by appealing to that organism’s specific goals and purposes, the mechanistic worldview that emerged during the Scientific Revolution assumed that organisms are simply machines and therefore can be understood by taking them apart to see how their ‘pieces’ work together to serve some purpose. Descartes explicitly states that organisms are *bêtes machines*, or, “animal/beast machines.” Among the more crude Cartesian doctrines, *bêtes machines* asserts the view that animals, “*bêtes*,” are soulless brutes devoid of reason, mind, or consciousness, and “*machines*” because their structure and function can be entirely understood by looking at the function and interactions of the parts (Walsh 2015).

Descartes’s machine model may be applicable to studying the physical and chemical properties of matter, like Newton’s laws of motion or Boyle’s discovery of the relationship between the volume and pressure of gas, because matter is inert and therefore does not change independently but reacts according to the influence of an outside force. Organisms, however, do not behave solely according to a set of universal, causal laws about the behavior of matter. For example, unlike matter or machines, organisms not only react, they respond. And, unlike matter, organisms can act and enact change without the influence of an external force. However, Descartes’s machine model and the analytic methodology it implies, when used to study organisms, obscures the characteristics of organisms that set them apart from machines and matter. Lewontin points this out when he argues that Descartes’s machine model is not simply an account of how the world operates but is also a “manifesto for how to study natural phenomena” (Lewontin 2000, 71). Therefore, if one wishes to study an organism as a machine, one must

commit oneself to the assumption that the organism “can be broken down into pieces whose identity as pieces is unproblematic and which have a clear chain of causal connections with each other in producing the properties of the whole” (Lewontin 2000).

The machine model for life and the analytic method that emerged from the Scientific Revolution are important landmarks in the history of science. They have been immensely helpful in providing a framework of the natural world that allows scientists to manipulate and predict it (Lewontin 2000). However, the machine model for life and the analytic method are not only frameworks, but they are also boundaries that inform concepts and methodology, which, in turn, determine the types of questions scientists can and cannot ask and the problems they can and cannot pursue. For example, the machine model for life and the analytic method also descend from and therefore carry the assumption that organisms are *bêtes machines*. This assumption that organisms are machines bounds the machine model and analytic method’s study of life by excluding the organismal processes and dynamics that set them apart from machines.

The Scientific Revolution is characterized by many important developments across the sciences that are landmarks in the history of science and continue to both implicitly and explicitly inform scientists’ work today. The emergence and rise of the machine model and analytic method were two important frameworks that developed during the Scientific Revolution and continue to inform contemporary scientific investigation that also reveal the Scientific Revolution’s emphasis on mechanism and reductionism. In the following subsection and continuing into Section 2, I will explore how this paradigm shift in the history of science towards a mechanistic conception of life informed the trajectory of the study of organisms towards a gene-centric paradigm by setting a precedent for studying organisms like machines, or, in terms of their component parts.

1.3.3 The machine organism set a precedent for studying organisms in terms of their component parts

Some of the central problems for biologists have been the question into the origin of similarities and differences between organisms, why offspring resemble their parents, and the mechanisms of development. Gregor Mendel (1822-1884), an Austrian biologist, meteorologist, and mathematician often referred to as the “father of genetics,” studied these questions through his exploration of hybridization in pea plants. Mendel refuted the prevailing blending theory of inheritance, which assumed that any characteristics inherited by progeny were an average of the parents' values of that characteristic, through his discovery that inheritance was governed by unobservable internal entities, which he called factors. Mendel used this discovery to formulate predictive principles of trait inheritance which were later termed the Law of Segregation, the Law of Independent Assortment, and the Law of Dominance. In 1866, Mendel published these findings, which opened space for the possibility that inheritance is particulate and atomic, since Mendel demonstrated that it appeared to be governed by the discrete heredity units he called “factors” (Walsh 2015). Mendel’s discovery of discrete heredity units reaffirms the notion that organisms are made up component parts, as suggested by Descartes’s machine model, and validates the analytic methodology because it was a discovery gained by looking at organisms’ constituent parts. This is not to say that there is not, in fact, genetic material being passed down from parents to offspring, but rather serves to demonstrate a significant scientific breakthrough in the history of science that provided evidence with which to justify the idea that organisms are made up of components.

Around the same time, Charles Darwin (1809-1882), who was not aware of Mendel’s work, published his theory of evolution in *On the Origin of Species* (1859). In *Origin*, Darwin

proposes that species change over time, species come from preexisting species, and all species share a common ancestor. Over the course of generations, Darwin claimed that populations evolve through the mechanism of natural selection, whereby those best adapted to their environment survive to reproduce while the ‘unfit’ are selected out. Natural selection is a variational account of evolution, whereby individual members differ from one another in some properties and evolve as a system through changes in the proportions of different types. Darwin’s variational evolution opposed and dismantled Lamarck’s transformational theory of evolution,⁸ which proposed instead that evolution was driven by changes in individual members that occurred during their lifetime (Levins and Lewontin 1985). One consequence of Darwin’s variational account of evolution is that it situates organisms as the *objects* of evolutionary forces because organisms themselves are not seen as undergoing evolution, but rather are situated as the “medium by which the external forces of the environment confront the internal forces that produce variation” (Levins and Lewontin 1985, 88).

Darwin did not explain in *Origin* how environments caused trait differences between individuals of the same species or how parents passed on these trait variations to their offspring. Darwin begins to address these gaps in the early 1860s when he and Herbert Spencer (1820-1903) translated the recently coined French term *hérédité* and introduced *heredity* into the English language (Keller 2010). Then, in 1868, Darwin published *The Variation of Animals and Plants Under Domestication* where he coined the term ‘gemmules’ to describe the internal

⁸ The “Darwinian” mechanism of evolution proposed a *variational* principle, “that individual members of the ensemble differ from each other in some properties and that the system evolves by changes in the proportions of different types” (Levins and Lewontin 1985, 86). Conversely, the “Lamarckian” mechanism of evolution proposed a *transformational* principle in regards to species’ changes because it assumed that each individual underwent variation, of which was assumed to be directly caused by and a specific response to an environmental cue (Koonin and Wolf 2009).

inheritance particles that are modified by the environment and passed down through generations, providing the mechanism for natural selection. Gemmules served as the units for Darwin's developmental theory of inheritance, which he named Pangenesis.

Under Darwin's influence, heredity began to take on its modern meaning, "referring not to external inheritance, but to the transmission of something biological, of some substance that resided within the body" (Keller 2010, 21). This simultaneous internalization and substantiation of heredity within the body sets the stage for the alignment between his notions of 'heredity' and 'innate' that would later be exploited by Galton to justify his racist anxieties (Keller 2010, 21, 28). Moreover, Darwin's newly-conceived units of inheritance (gemmules) were situated as responsible for the variation between organisms. This atomization of inheritance and evolution by natural selection reduced the organism to the role of a gemmule-container and the vehicle of inheritance, which presents evolution by natural selection as a genetic theory, rather than a theory about organisms themselves.

Darwin's notion of a particulate kind of heredity took on an even more atomistic character when his cousin Francis Galton (1822-1911) assigned gemmules an invariant character. While Darwin supposed that gemmules could be shaped by organisms' experiences, Galton situated gemmules as fixed entities that were passed throughout generations without change (Keller 2010). Furthermore, Galton's view that heredity is a structure residing in discrete, unchanging entities aided Galton in his coining of the phrase "Nature and Nurture" (1874), where he leveraged the assumption that the units of heredity are innate and not influenced by the environment in order to bond "nature" to heredity (Bliss 2018; Keller 2010). Before Darwinian evolution and Galton, the terms "nature" and "nurture" were neither separate nor opposed (Bliss 2018). However, Galton's phrase "Nature and Nurture" "conjoins two domains on the tacit

assumption that they are initially disjoint” (Keller 2010, 16). ‘Nature,’ in this sense, is taken to mean innate or genetic, whereas ‘nurture’ signifies acquired or environmental; disjoining the two forces implies that they exist in separate realms, which Keller argues is predicated on an opposition (Keller 2010). This divide is both temporal—‘nature’ is assumed to take place before birth as “all that a man brings with himself into the world,” whereas ‘nurture’ is defined as “every influence that affects him after birth”—and substantive—i.e., as a difference between the two types of “elements of which personality is composed” (Galton 1874, 12).

Galton and his deterministic notion of genes became especially influential in the late nineteenth century and fit perfectly into his pseudoscience of eugenics which he propagated through the use of twin studies (Bliss, 16). These twin studies, popularized by eugenics and a particulate notion of inheritance, formalized the definition of heritability as the “percentage of variance in a population due to genes” (Winerman 2004, 46, quoted in Bliss 2018, 16). Bliss reveals that the formalization of this notion of heritability implied the strict split in the terms “nature” and “nurture,” which was popularized by the eugenics manifesto that genes and environments were separate forces, with genes being the more dominant of the two (Bliss 2018).

Separating, opposing, and creating a hierarchy between nature (internal, innate; genetic) and nurture (external, acquired; environmental) is a mistake because it supposes that genes and the environment individually have causal powers to affect developmental processes (Keller 2010). In reality, however, genes cannot shape development in the absence of environmental factors, and neither can environmental factors in the absence of genes (Keller 2010).

Developmental processes, rather, are entangled, dynamic interactions that cannot be separated to discern mechanistic causality because development depends on the “complex orchestration of multiple courses of action that involve interactions among many different kinds of elements—

including not only preexisting elements (e.g., molecules) but also new elements (e.g., coding sequences) that are formed out of such interaction, temporal sequences of events, dynamical interactions, etc.” (Keller 2010, 6-7). Nonetheless, Galton’s prioritization of nature over nurture set a precedent that genetic factors are not only separable from environmental factors, but that genes are the more important force to consider when studying development. Galton’s disjoining of nature and nurture and prioritization of nature served his eugenicist agenda by aligning genes and race. Under the guise of science, Galton’s agenda that an individual’s genes are more important than their environment has been weaponized throughout history to naturalize systems of oppression, disincentivize and underfund social services and other forms of public goods like public education in favor of investing in genetic research, take responsibility off institutions for erecting and maintaining systematic barriers, justify “scientific” racism, among other offenses.

In 1900, Mendel’s laws were rediscovered. Mendel’s experimental system, terminology, and notation served as examples to study variation and heredity, which William Bateson named “genetics” in 1905, and played an important role forming the concept of the gene (Meunier, 2002). Darwin’s theory of Pangenesis was replaced in 1893 by August Weismann’s germ line theory—the Weismann doctrine (Figure 1)—which argued that inheritance can only occur through germ cells (gametes, like egg and sperm cells) and not by somatic cells (cells that form organs or tissue, for example).

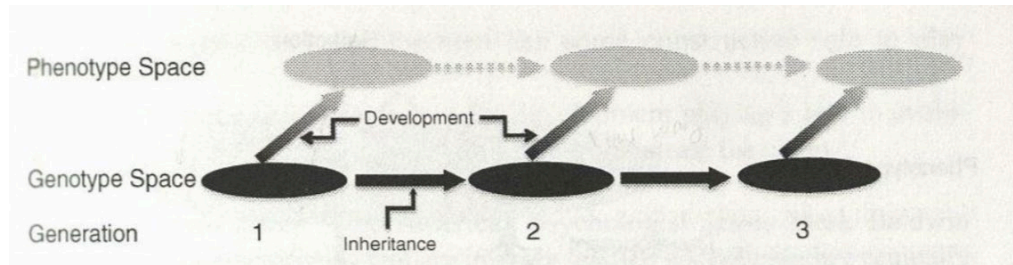


Figure 1: A version of the ‘Weismann diagram.’

Development maps genotype space onto phenotype space, but genotype space itself goes unaltered by development. Inheritance also only takes place in genotype space. Accordingly, genotype space and phenotype space exist in discrete realms. Figure caption adapted from and figure from Walsh 2015.

Weismann’s theory reinforced the dichotomy between innate and acquired characteristics and promoted the idea that development is a unidirectional, linear process that can only begin in the germ cells (Walsh 2015). This led to the fractionation of the four evolutionary processes because it assumed that the only source of evolutionary novelties had to come from the germ line (Walsh, 78). Germ line theory also dismantled Darwin’s concept of “gemmules”—the particulate yet environmentally-shaped units of inheritance—by arguing that inheritance only takes place through the germ cells. This further supported the alignment between “innate” and “hereditary.” Darwin’s gemmules were replaced by Mendel’s “factors,” which were then replaced by the concept of the “gene,” first coined in 1909 by Wilhelm Johannsen (1857-1927). Johannsen’s idea of the gene was meant to “express merely the simple idea that ‘something’ in the gametes can condition or take part in the determination of a property of a developing organism” (Meunier 2022).

Leading up to the early twentieth century, there were two distinct groups, the biometricians and the Mendelians, with competing viewpoints regarding the mechanism of evolution. The biometricians’ account of evolution was a theory of adaptation, positing that adaptive evolution took place through individuals’ gradual, continuous accumulation of small

improvements by Darwinian natural selection (Walsh 2015). Conversely, the Mendelians held that evolution happens through the process of lineage change and stasis. Instead of evolutionary change happening continuously at the individual level, the Mendelians cited the fact that inheritance is mediated by ‘factors’ that are passed from parents to offspring and usually go unaltered as they are passed down (Walsh 2015). Furthermore, the Mendelians asserted that evolutionary change happens through the introduction of new factors through mutation, and argued that inherited differences between individuals are too “course-grained and discontinuous to provide the minute and graded heritable differences between organisms” required by the biometricians (Walsh 2015, 55).

In 1918, R. A. Fisher⁹ (1890-1962) published his seminal paper “The Correlation between Relatives on the Supposition of Mendelian Inheritance,” which resolved the debate between the Mendelians and biometricians by demonstrating that Mendelian inheritance is compatible with Darwinian natural selection (Walsh 2015). Fisher’s paper, along with his book *The Genetical Theory of Natural Selection* (1930) helped reconcile neo-Darwinism with the Mendelian model of inheritance through the Genetical Theory of Natural Selection—the theoretical fuel for the Modern Synthesis theory of evolution (Walsh 2015). Fisher leveraged the statistical framework of thermodynamics to create a model of natural selection: while Darwin pictured the object of evolution to be a population of individual organisms, Fisher’s object of evolution was a much larger collection of “indefinitely many abstract entities” which he called

⁹ The English mathematician R. A. Fisher continued Galton’s work by attempting to distinguish between genetic and environmental influences (Keller 2010). This was certainly a challenging feat, and, like Galton, Fisher felt that eugenics was needed both scientifically and socially to address the question (Keller 2010). In 1911 when Fisher was still a student and before he published in 1918 paper, he formed the Cambridge University Eugenics Society with the help of John Maynard Keynes, R. C. Punnett, and Charles Darwin’s son (Keller 2010).

“gene types” or “gene ratios” (Fisher 1930, 34; Walsh 2015, 55). Explaining the Fundamental Theorem of Natural Selection, Fisher writes:

[The Fundamental Theorem of Natural Selection is] The rate of increase of fitness of any [population] at any time is equal to the additive genetic variance at that time....It will be noticed that the fundamental theorem...bears some remarkable resemblances to the second law of thermodynamics. Both are properties of populations, or aggregates, true irrespective of the nature of the units which compose them; both are statistical laws; each requires the constant increase of a measurable quantity, in the one case the entropy of a physical system and in the other the fitness...of a biological population. (Fisher 1930, 35-36)

This account of evolution is distinctly population minded. While individuals figured into Darwin’s account of population change as “*lineages of organisms*” within a population as a function of their success in their struggle for existence, Fisher’s theory of natural selection “plots the change in *intrinsic growth rate* of an indefinitely large population of *abstract ‘gene ratios,’* as a function of its statistical distribution of growth rates” (Walsh 2015, 57). As such, Fisher’s theory put biological evolution into abstract, physical, and statistical terms. Since Fisher’s theory was so pivotal in motivating the Modern Synthesis theory of evolution, its framework in many ways also established a precedent in the biological sciences, and specifically evolution, for studying organisms’ evolution from physical, rather than biological, perspective, as Fisher did, and in terms of changes in populations and genes.

It is important to note that there are certainly other frameworks within biology, and specifically genetics and evolutionary biology, that have also emerged out of the Modern Synthesis era but are not as focused on population dynamics. For example, quantitative genetics diverges from the population genetics because it explores how variation in an individual’s genotype and environment contributes to phenotypic variation among individuals (O’Brien 2015). Nonetheless, both population genetics and quantitative genetics explore their respective areas by focusing on their genetic basis (O’Brien 2015; Sheehy and Johnson 2014), and emerged

out of the Modern Synthesis evolutionary theory that came out of the twentieth century, which came with an emphasis on investigating the genetic basis of evolution (von Cramon-Taubadel 2019).

Conclusion

This section considered some of the important developments leading to the Modern Synthesis and the scientists whose work was important in setting the stage for this shift in the history of science towards a gene-centric paradigm. Considering these shifts is important because it reveals that the gene-centric paradigm did not simply materialize from an impartial and value-neutral realm, but emerges from a lineage of scientific thought as it is embedded in a particular cultural moment and reflective of choices made by individuals who are, too, formed by their socio-historical-cultural positionality. As such, this section helps contextualize Section 3 by clarifying and connecting some of the important scientific developments and assumptions that laid the groundwork for the gene-centric paradigm's rise to prominence in the twentieth century.

Section 2

Section 1 laid the groundwork for Section 2 by contextualizing important scientific developments that helped facilitate the emergence of the gene concept and the gene-centric paradigm. Section 2 continues this exploration by considering the understanding of the gene's structure and functioning that gained traction in the twentieth century and helped catalyze the molecularization of biology and reinforce gene-centrism's rise to prominence. In this section, I will characterize the notion of genes that emerged during the twentieth century by exploring the metaphors and other language used to describe gene action. Through this exploration, I demonstrate that the gene concept that emerged during the twentieth century reinvokes the mechanistic, deterministic, and reductionistic representation of life that was so popular during the Scientific Revolution by drawing on computational metaphors and experiences with machines. I continue this discussion by exploring the ways in which this mechanistic language, in turn, shapes the ways in which we understand organismal processes by representing life using the analogy of a machine.

I then go on to explore how the mechanistic notion of genes that emerged during the era of the Modern Synthesis motivated a shift in the biological sciences to research that prioritized studying organisms in terms of their genetic elements. These approaches that use an individual's genes as a lens through which to understand the whole organism are what I refer to as "gene-centric" methods. I will analyze and characterize the features of gene-centrism in order to explore its scope, strengths, limits, and underlying assumptions as a method of scientific inquiry and an indicator of a larger paradigm. This analysis leads me to a survey of the gains under gene-centrism, and an analysis of the three major limitations and explanatory gaps of gene-centrism as

a method of studying organisms. In Section 3, I will then go on to explore how these limitations suggest the need for a complementary approach to studying organisms.

2.1 Machines and metaphors

It is impossible to practice science and formulate biological explanations without the use of a language filled with metaphors that attempt to grasp the meaning of complex concepts, processes, and relationships by comparing them to something commonly understood (Keller 2010; Lewontin 2000). These metaphors attempt to explain and conceptualize phenomena that are too small or too vast for humans to directly perceive or experience by “appeal[ing] to the understanding of the world that we have gained through ordinary experience” (Lewontin 2000, 3). In the case of genes, biologists often describe these elusive entities by comparing them to “recipes,” “programs,” “codes,” or “blueprints” (Lewontin 2000; West-Eberhard 2003). These metaphors, intended to offer a way of conceptualizing biological processes, are informed by everyday experiences, which then reciprocally shape scientific practice by informing the metaphors used to describe phenomena. As such, the metaphors we use to describe genes do not *only* offer a way to understand what genes are and how they work; the metaphors we use are shaped by our experiences and therefore *also* provide a glimpse into the ways in which our everyday experiences inform biological explanation (Talbot 2012).

The gene concept emerges from “our experience with machines” and occupies the metaphorical language of causal analysis whereby the scientist’s role is to examine the way certain parts fit together to contribute to the functioning of hierarchical system, giving us a pieced-together knowledge of the integrated whole through explanatory mechanisms of the parts (Talbot 2012, 51). For example, during the Scientific Revolution, Descartes’s machine model provided a metaphor to help explain organismal life by comparing it to a machine. Comparing

life to a machine also came with a program for how life should be studied; assuming that life is a machine, as the metaphor posits, justifies the analytic method and mechanistic decomposition as a means to studying life because the metaphor assumes that, like machines, organisms can be separated into constituent parts that interact with one another to make the system function (Lewontin 2000). The understanding of the gene's structure and function that arose during the twentieth century paralleled the formation of the digital computer (Walsh 2015). Similarly to the way that Descartes's machine model proposed an explanation for life and a manifesto for the way it should be studied (Lewontin 2000), the development of the digital computer offered a research strategy and helpful metaphors through which to explain organisms and their processes (Walsh 2015). For example, computation provided a metaphor to describe development as "the process in which the instructions encoded in the genes is implemented" (Walsh 2015, 114).

The metaphor of a genetic program that gained traction in the twentieth century reinforced the classical notion of the gene as a unit of phenotypic control because it compared development to a computation whereby genes are discrete, context-independent "causal agents" coding for specific phenotypes (Walsh 2015, 128). Richard Dawkins exemplifies this orientation around genetic determinism and the concept of genes as "units of control over biological form" (Walsh 2015, 68) when he describes protein-coding DNA sequences, or genes, as "code symbols" that are translated from "strictly sequential DNA ROM [read only memory]" into a predetermined, "precisely invariant three-dimensional protein shape" (Dawkins 1986, 171). In this story, DNA is situated as a sequence of zeros and ones that is passively translated, forming a predetermined protein shapes which, according to Dawkins's linear and unidirectional representation of translation, are rigid in their structure and incapable of changing. These computational metaphors also reinforce the notion of the machine organism because they rely on

mechanistic language to describe life, situating organismal development as the execution of a gene program and phenotypic outcomes as outputs of a predetermined gene code (Walsh 2015).

The twentieth century discovery of the structure of DNA and its role as a protein-specifying molecule shaped and built confidence around the assumption that an organism's DNA sequence is a "self-contained phenotypic script or 'blueprint'" (Sultan et al. 2021). This deterministic notion of genes crystalized around the metaphor of development as the execution of an organism's internal phenotypic script (Sultan et al. 2021). Understanding genes as codes and development as the execution or computation of those codes helped catalyze a paradigm of gene-centrism across the biological sciences, and especially during the twentieth century (Sultan et al. 2021). Comparing development to a computation gives genes a privileged status in the formation of traits because the comparison operates under the assumption that development is a linear program whereby one can determine phenotypes by simply computing the information encoded in the genes. The idea that development is a linear process beginning with the information encoded in genes is epitomized by the Central Dogma of molecular biology, coined by Francis Crick:

The central dogma of molecular biology deals with the detailed residue-by-residue transfer of sequential information. It states that such information cannot be transferred back from protein to either protein or nucleic acid. (Crick 1970, 561, quoted in Walsh 2015, 79)

The Central Dogma suggests that inheritance is a unidirectional process beginning with, and solely dictated by, DNA. While it does not explicitly mention the relationship between inheritance and development, the Central Dogma implies a deterministic, linear causality between the two—DNA guides protein synthesis, but protein synthesis does not effect changes in DNA structure (Walsh 2015) (Figure 2.1).

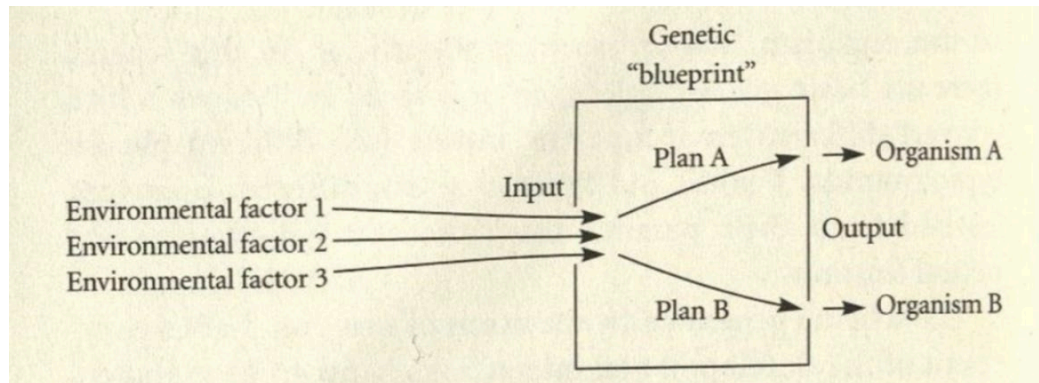


Figure 2.1: Representation of the genetic determination of the organism.

Environmental factors enter the organism's "Genetic 'blueprint'" like an input into a computer. Since the organism is determined by its genes, there is no interaction between environmental and genetic factors; the extent to which environmental factors input into organisms to produce different outputs is determined by the organism's "Genetic 'blueprint.'" Figure from Lewontin 2000.

If DNA structure, providing the developmental instructions for the process of inheritance and protein synthesis, is assumed to be the process of development, then the Central Dogma reinvokes the Weismann doctrine's fragmentation of inheritance and development (Figure 1) by asserting that the units of inheritance (genes) are unaltered by developmental processes (Walsh 2015). Consequently, the Central Dogma maintains that inheritance and development are discrete processes and also provides the distinction between genotype and phenotype that is so important to the Modern Synthesis (Walsh 2015) (Figure 2.2).

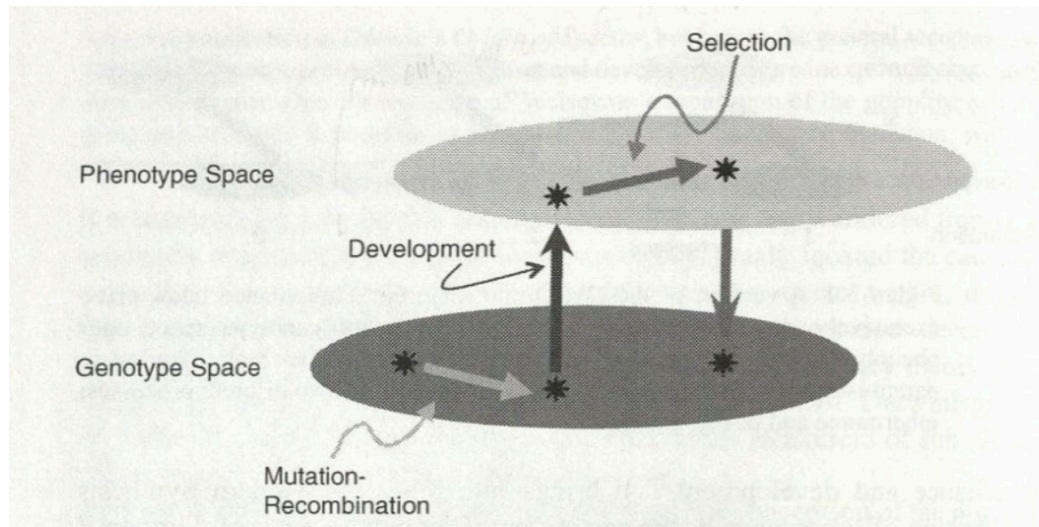


Figure 2.2: Evolution in genotype and phenotype space.

Genotype space and phenotype space are separated to illustrate the idea that they are separable and discrete instead of interconnected and continuous. The separation of genotype space and phenotype space also visualizes the idea that there is a linear, one-to-one relationship from genotype to phenotype instead of a reciprocal relationship. “Development” points from genotype space to phenotype space to suggest that development induces no changes in genotype space, reinforcing the idea that organisms’ genes are not environmentally insensitive but determined. Figure from Walsh 2015 as adapted from Lewontin 1974.

The Weismann doctrine cleaves the processes of evolution because it is based on the assumption that changes in the body during development do not elicit changes in the germ cells and that “inheritance is...exhausted by the transmission of germline material” (Walsh 2015, 79). Similarly, Modern Synthesis evolutionary theory gives genes a privileged status in the formation of traits, which also contributes to the fractionation of the four evolutionary processes in its theory of evolution (Walsh 2015, 79) In this view, the origin of evolutionary novelties, for example, can only arise due to mutations, making them unaffected by adaptive processes, development, and inheritance (Walsh 2015). Similarly, while offspring develop the phenotypes specified by the genes they inherited from their parents, development itself cannot affect the inherited information (Walsh 2015). Selection also relies on the processes of inheritance and

development, but it alone does not alter them; rather, selection “winnows organisms, discerning between the existing range of inherited replicators and developmental processes” (Walsh 2015, 74).

2.2 What is gene-centrism?

During the twentieth century, our experiences with machines helped provide metaphors to begin to represent and grasp biological processes that had previously gone unaccounted for. As I explored in the previous subsection, the use of computational and mechanistic metaphors to describe genes and, more broadly, organismal life, justified a deterministic understanding of gene action. In this subsection, I will consider some of the ways in which this deterministic understanding of gene action has methodological consequences.

Across biological disciplines, the deterministic notion of genes that rose to prominence during the era of the Modern Synthesis has validated and motivated a shift in research focus in the biological sciences to one that emphasizes studying genetic elements as a means to understanding phenotypes and their variations among individuals (Sultan et al. 2021). The Human Genome Project is a prominent case that shows up in the literature as an example of wide-scale genetic determinism that reveals the paradigm of gene-centrism. The researchers working for the Human Genome Project themselves demonstrated that the project is indicative of a gene-centric paradigm when they compared the project to the Apollo moon landing and the splitting of the atom, stating that they foresaw the dawn of a new era, “the era of the genome” (*National Human Genome Research Institute* 2012, quoted in Gannett 2008). That being said, to simply say that the paradigm of gene-centrism motivated a shift in research focus in the biological sciences towards more gene-centric biology, and even genetic deterministic biology, might even be an understatement. The prevalence of the Human Genome Project, and the degree

to which it (and similar genetic deterministic studies) was met with such high expectations by scientific and the public alike suggest that the project may have oversaturated biological research and even discouraged less gene-focused studies by shifting funding priorities.

Approaches that embrace an organism's genetic elements as a lens through which to understand some part of the organism—such as those modeled by the Human Genome Project—are what I refer to as “gene-centric” methods. What characterizes a gene-centric or part-to-whole approach? I want to preface my explanation of gene-centrism by saying that gene-centrism is a paradigm and also a practical framework for studying organisms. Much like the metaphors we use to explain elusive scientific concepts are both informed by commonly understood experiences and also used at a practical level to help us do science, gene-centrism is both paradigmatic and practical. For example, as I explained in Section 2.1, the gene concept and the metaphors we use to explain the gene are paradigmatic and practical; many of the metaphors we use to explain the gene and study it scientifically are intimately informed by and reflective of a particular cultural moment and concepts that people resonate with and understand. In the case of the gene, the emergence of computers helped provide a language through which to depict these elusive entities. However, much like comparing a gene to a code makes certain assumptions about the gene itself and the organism of which it is a part, scientifically studying organisms using a gene-centric framework requires that one make certain assumptions about the organism, many of which I will go on to explain in this section and throughout this thesis. Many of these assumptions are already implied in the gene-centric methodology and in the greater framework of the Modern Synthesis, which means that individuals using this methodology in a practical setting might not be inclined, or never given the tools, to inquire into the broader cultural/paradigmatic assumptions of organismal life implicitly informing the gene-centric

framework they use. In my experience of learning about and doing science, the biological theories, metaphors, and methods I have been taught are rarely, if ever, taught in a way that critically explores the scientists from which they came and the ways that those scientists' assumptions and particular socio-political-historic context may be implicit in the theory, metaphor, or method they are credited for developing. When I learned about Galton's contributions to Darwin's work, for example, I was taught that Galton popularized the nature-nurture debate. However, I was not taught that Galton's separation of nature (genes) and nurture (environment) and his conclusion that nature has a larger effect than nurture on development was *also* fueled by and used to justify his eugenicist agenda. This example serves to demonstrate that there is, indeed, an intersection between paradigm and practice, and lived experience as it goes on to inform how biological concepts are characterized, taught, and go on to shape biological scientific methodology and inquiry. That being said, I think it is important to begin exploring the ways in which paradigm and practice share an intimate relationship that is both reciprocally informative and reproductive, while also recognizing that gene-focused approaches, when conducted in the lab at the individual level, are not necessarily intended to reproduce or carry the assumptions associated with the paradigm as a whole, or the particular assumptions and biases of the scientist(s) from which they came.

Gene-centrism offers what Sultan, Moczek, and Walsh (2021) call a component-to-system direction of explanation because it begins at the organism's genetic parts, or, components, and looks at how their activities and interactions influence the system as a whole. This direction of explanation employs a mechanism perspective that descends from the methodology of mechanism that inspired the Scientific Revolution (Walsh 2015). The mechanistic viewpoint adopts the analogy of a machine to describe its object of study because it

assumes that the object of study, though it may be created to execute a specific function, operates the way it does because of the inner-workings of its parts. Relying on this mechanistic methodology, the component-to-system direction of explanation assumes that the organism's genetic make-up dictates—and therefore be used to predict—how that organism is inclined to develop or behave under certain circumstances (Walsh 2018). Since mechanistic methods work in the component-to-system direction to attempt to discern the causal processes and organization that enable it to perform a specific function, these methods typically rely on decomposition as an explanatory strategy and have the characteristics of reductionism (Walsh 2015). While the epithet 'reductionism' tends to be stigmatized in the philosophy of science, I use the term without intending to invoke these stigmas or criticize reductionism as a method. Instead, I want to point out the connection between mechanism and reductionism in order to demonstrate that the methodology of mechanism proceeds as a kind of reductionism because it investigates organismal systems by looking at the structure and functioning of their genetic parts (Walsh 2015).

According to Lewontin (2000), reductionism, employing the analytic methodology, begins by deconstructing the whole into its members in order to elucidate the causal relationships between members. In the case of molecular biology, as Lewontin points out, the object of investigation is the interactions between molecules; for example, clarifying the mechanism by which proteins are synthesized from information coded in DNA sequences (Lewontin 2000). Conducting such a molecular study requires that one decompose and reconstruct the system into the appropriate “pathways of causal connection between molecules because there is no collection of molecules that can be known *a priori* to form a relevant functional unit” (Lewontin 2000, 77). This example exemplifies the reductionist method because it uses a downward analytic process

to break molecular pieces into their parts, which is followed by a synthetic phase where the causal relations and pathways between the pathways are uncovered (Lewontin 2000).

Reductionism as a methodology is not inherently the issue here. Rather, it is that there is no obvious way to use reductionism to decompose organisms into constituent parts because their internal heterogeneity makes it so that a meaningful part cannot be defined without first defining the functional whole of which they are members (Lewontin 2000).

2.2.1 Gene-centrism is an object theory

Since gene-centrism relies on a reductionist, mechanistic component-to-system direction of explanation to investigate organisms, gene-centrism is an *object theory* (Walsh 2018). The domain of object theories, as the name suggests, is limited to describing objects. The goal of an object theory is to investigate and explain the objects' dynamics and possible trajectories as they are subject to external "forces, laws, and initial conditions" that exist independently of the object (Walsh 2015, 212). Since gene-centrism is an object theory, and because objects are the domain of object theories, gene-centrism accounts for organisms as objects. According to Walsh (2018), objects are "constituted of matter and take their definitive properties from their material constitution. These definitive properties are generally thought of as intrinsic dispositions, propensities to behave in certain ways when they encounter certain external conditions" (168). Through this definition of objects, Walsh implies that object theories tend to approach the object of study from a physiochemical perspective because they assume that the object itself is the composite matter, which is both passive and inert and therefore implies a lack of biological activity. Since objects are made of matter and because matter is inert, objects themselves cannot enact or spontaneously respond to conditions but only react to being acted on by an external force. Accordingly, object theories reduce organisms to the *objects* of their material constituents

since their ability to exist in the world is dictated by the properties of their material (genetic) make-up; instead of embodying their genes, the organism passively encases them, serving as a medium by which internal (genetic) and external (environmental) factors connect. This also implies that object theories are context insensitive because they do not account for the ways in which the object's functioning as an entire system may reciprocally affect the dynamics of its parts (Walsh 2015).

Walsh's definition of objects as "taking on definitive properties from their material constitution" reiterates the context-insensitive nature of component-to-system object theories like gene-centrism. In addition to revealing object theories' context-insensitivity, Walsh's definition also shows that object theories cannot account for the ways in which relationships or interactions might constitute or reconstitute objects. In order for object theories to assume that an object's properties are predictable based solely on the properties of its material constituents, they must either leave out the object's environmental context or hold the environmental context constant. Under constant conditions when the environment is not changing, the object will react predictably. But if its context changes, the object, being made of matter with definitive properties, will only be able to predictably react to the extent to which its properties allow until it will eventually reach a context in which it can no longer react, at which point the object will cease to exist because it cannot take on its definitive properties. For example, if a watch's 'definitive property' is to tell time and you took a non-water resistant watch and put it in water, it would continue telling time until the gears became waterlogged and it eventually breaks. Once the watch can no longer tell time as its gears have been built to do, it can no longer execute its 'definitive property' as a time-telling machine because its parts have exceeded their working capacity. Furthermore, the watch's gears are unresponsive to the change in environment because

objects are context insensitive; this supposes that definitive properties (the watch's ability to tell time) are intrinsic, meaning that "nothing other than the internal constitution of the entity itself could confer on its causal powers" (Walsh 2015, 220). Similarly, since object theories posit that objects operate solely by virtue of their 'intrinsic dispositions,' objects will react predictably because their reactions are determined by the capacity of parts, not by the capacity of the aggregate of such parts or by a synthesis of influences from both their parts and their context.

Another aspect of the component-to-system approach's context insensitivity is the implicit assumption that changing one part of the system will not elicit compensatory changes in the other parts (Walsh 2015). This is a logical and appropriate assumption to make when using a component-to-system approach to study an actual object. For example, removing a gear from a watch would not cause the watch to 'regrow' the missing gear or change its structure or function in any way to compensate for the removal of one of its parts. Similarly, if a scientist using a component-to-system approach were to engineer the removal of a gene known to code for a specific phenotype, they would not expect changes in other genes or molecular processes but instead would be inclined to look for these effects by potential changes in that phenotype.

2.3 Scientific gains under gene-centrism

Approaches to studying organisms that leverage genes as a lens through which to understand organisms offer a component-to-system direction of explanation. Gene-centric approaches offer a component-to-system direction of explanation because they focus on clarifying how the organism's genetic parts and their dynamics influence the functioning of the system as a whole. While the interactions between the parts of a complex system may not always provide an exhaustive explanation of the system's functioning, as is the case for organisms, an organism's genetics certainly play a crucial role in their development and evolution. Therefore,

the component-to-system method can offer scientists indispensable insights into the nature of life, as it has certainly done. Focusing on genes and genetic variants has helped facilitate the development of an explanation of some of the most complex organismal systems and processes in terms of the mechanistic, causal interactions of complex molecules, making twentieth-century biology the “triumph of reductive mechanism” (Walsh 2015, 30-31). Gene-centric approaches have furthered scientific knowledge of molecular signaling pathways, helped in identifying genetic variants involved in disease which aids in tailoring medical interventions, progressed genetic engineering technology, and clarified phylogenetic relationships and histories (Sultan et al. 2021).

A prevalent gene-centric tool that follows the component-to-system assumption that there is a predictable, straightforward relationship between genotype and phenotype is genome-wide association studies (GWAS). GWAS attempt to find the statistical association between genetic variants and specific phenotypes. The goal of GWAS is to “uncover the underlying molecular mechanisms by which a disease originates, and in particular, identify all relevant genes and gene variants (i.e., *disease causality*)” (Pierce et al. 2020, 1, quoted in Sultan et al. 2021, 2). The GWAS approach has identified some important associations between genetic variations that may contribute to phenotypic outcomes, such as type 2 diabetes, Parkinson’s disease, heart disorders, obesity, Crohn’s disease, and prostate cancer, to name a few (*National Human Genome Research Institute* 2020). If this technology is made more accessible to individuals from different racial and ethnic backgrounds and is equitably affordable and available, GWAS will, ideally, inform patients of their risk of developing certain diseases which may help medical professionals develop more personalized and preventative care plans.

During the twentieth century, the Modern Synthesis's gene-centric approaches were instrumental in explaining biological processes by revealing their molecular mechanisms. For example, they aided in the discovery of DNA, the development of genome-sequencing technology, and furthered knowledge about protein synthesis and the biochemistry of metabolism (Walsh 2015). The molecular revolution of the twentieth century was also instrumental in providing a simple yet powerful genetic concept of evolution. In Darwin's theory of evolution, the organism is the fundamental unit of organization; organisms, by struggling for their existence, engage in the activity that creates the conditions necessary for evolution to occur (Walsh 2015). During the twentieth century, however, the discovery of DNA as a protein-specifying molecule helped form the impression that genes encoded the phenotypic information needed to build organisms, therefore making genes the "ultimate difference makers" in determining organisms' evolutionary traits (Walsh 2015, 72). In the account of evolution that came out of the Modern Synthesis, genes, or 'replicators,' as Dawkins (1976; 1982) calls them, became the fundamental unit of organization (Walsh 2015). This commitment to genes in the Modern Synthesis theory of evolution, coupled with the Central Dogma's isolation of genotype space from phenotype space and the assumed unidirectionality from genetic inheritance to phenotypic development, situated genes as the units of evolutionary change. As a result, evolution came to be understood as a change in genes' frequencies in a population over time. This perspective was instrumental in fractionating the four processes of evolution—mutation, migration, genetic drift and natural selection—enabling biologists to examine each process as discrete and quasi-independent, with each process having a distinct cause (Walsh 2015). The separation of the evolutionary processes is practically helpful to biologists because it allows one

to one evolutionary process without needing to take the other three processes into account (Walsh 2015).

2.4 Limitations of gene-centrism

While gene-centric approaches have been incredibly productive to the study of life, Sultan et al. (2021) reveal three major explanatory gaps of gene-centric, component-to-system approaches regarding (1) phenotypic variation; (2) trait transmission from parents to offspring; and (3) the origins of novel, complex traits (Sultan et al. 2021). In this subsection, I will explain how gene-centric approaches that rely on genetic components as the single lens through which to understand development, inheritance, and evolutionary innovation result in these three explanatory gaps.

2.4.1 Explanatory Gap 1: Phenotypic variation: The landscape between genes and phenotypes is neither direct nor linear

The first gap challenges the viability of using causal chains¹⁰ to deduce a supposedly linear relationship from genotype to phenotype by revealing that the one-to-one mapping of genotype to phenotype is actually much more complicated (Sultan et al. 2021). Therefore, genotypes cannot be used to determine phenotypic outcomes and individual variation (Sultan et al. 2021). GWAS, in attempting to discern disease causality by identifying statistical associations between genetic variants and phenotypes of interest, exemplify the gene-centric assumption that there is a

¹⁰ Causal chains are systems in which every downstream product relies on there being previous inputs(s) and outputs(s) (Ross 2021). Sometimes causal chains are called ‘domino causality’ because the effect of one step becomes the cause of the next, much like in a series of successively falling dominoes (Ross 2021). “Causal chains are usually *ceteris paribus*,” meaning that they usually assume that all other things are equal—one variable might have an effect on another, assuming that all other variables remain constant; a gene might result in a specific phenotype, assuming that individuals with this gene are all raised in the same, unchanging environment (Lewontin 2000, 95).

causal, straightforward relationship between genotype and phenotypic outcome (Sultan et al. 2021). GWAS, however, are quite limited in their overall ability to explain phenotypic differences from a genetic basis and therefore exemplify the first explanatory gap in gene-centric approaches: phenotypic variation (Sultan et al. 2021).

It is highly unlikely that GWAS will ever be able to explain or accurately estimate 100% of the heritability of complex traits (Tam et al. 2019). Nonetheless, the phenotypic variation that GWAS *has* been able to explain is surprisingly limited (Haines et al. 2009). Genetic variants associated with late-onset Alzheimer’s disease, for example, have been recognized at numerous loci but the heritability and disease risk is only moderately predictable based on genotype (Bertram et al. 2010). Similarly, human height is associated with at least 40 loci and has a heritability of 0.8, meaning that approximately 80% of the variation in height among individuals in a population is due to genetic factors (Visscher, 2008). Despite its high heritability and the fact that these results draw from statistically promising studies of tens of thousands of people, the genetic variants for height can only explain about 5% of height variation among individuals (Visscher, 2008). GWAS’ limited ability to explain height variation also reveals that GWAS are not necessarily able to identify causal variants and genes (Tam et al. 2019). In the case of height, simulations have shown that 90,000-100,000 single-nucleotide polymorphisms¹¹ (SNPs) may be required to explain its 80% heritability, meaning that a serious amount of all genes may contribute to variation of complex traits (Tam et al. 2019). Since GWAS identify so many genes

¹¹ A molecule of DNA is composed of two strands that are zipped together (Harden 2021). The strand can zip together because it is made up of interlocking pairs of four different types of nucleotides: guanine (*G*), cytosine (*C*), adenine (*A*), and thymine (*T*). A single-nucleotide polymorphism, or SNP (pronounced “snip”), is a type of genetic difference between people; “some people have one nucleotide at a particular spot (locus) in their genome, whereas other people have a different one. You might have a *G* whereas I have a *T*” (Harden 2021, 58). The variations of the SNP are called *alleles* (Harden 2021).

that are potentially involved, the risk is that this number may be too high to be helpful in predicting outcome (Tam et al. 2019).

The recently proposed ‘omnigenic’ model posits that for complex traits, association signals can be dispersed throughout the entire genome, and potentially near genes who do not share any obvious connection to disease (Boyle et al. 2017). This suggests that gene regulatory networks are interconnected such that all genes expressed in disease-relevant cells may impact the function of significant disease-related genes, and that most variation and heritability can be explained by genes outside of the primary pathways (Boyle et al. 2017; Tam et al. 2019).

Addressing the limitations of GWAS has also come in the form of studies that address more than just the genetic association with phenotypic outcome by directly targeting environmentally sensitive pathways that modulate gene function, and hence may be phenotypically relevant, in order to explore gene-environment interaction effects (Zhu et al. 2014). Other context-dependent studies have examined the role of environmentally mediated epigenetic changes (Skinner, 2014), as well as systems like an individual’s microbiome composition which dynamically responds to changes in the individual’s environment, such as diet, behavior, or social context (Sandoval-Motta et al. 2017, quoted in Sultan et al. 2021).

2.4.2 Explanatory Gap 2: Trait transmission from parents to offspring: Transmission of specific genetic variants cannot completely explain or predict the phenotypic impact of biological inheritance

Since gene-centric approaches operate in the component-to-system direction to explain organismal processes, they can only offer a genetic account of inheritance. However, numerous studies have shown that organisms inherit phenotypic information not only from their parents’ genes, but also from environmentally induced regulatory effects, revealing the second

explanatory gap of gene-centric approaches: “trait transmission from parents to offspring” (Sultan et al. 2021, 3). The second explanatory gap reveals that an organism and its genes are shaped in part by its environment. Many of these environmentally induced genetic changes are heritable, which means that offspring not only inherit their parents’ genes, but their parents’ environment. The idea that inheritance is not completely genetically determined but environmentally shaped adds another layer of nuance to the concept of biological inheritance that a component-to-system direction of explanation cannot account for.

The discovery that DNA has a protein-specifying code—the Central Dogma of molecular biology—helped biologists explain that offspring resemble their parents because they inherit their parents’ developmental instructions in the form of genes (Sultan et al. 2021). As mentioned in the Section One, Galton’s particulate notion of genes and inheritance and his separating and opposing of ‘nature’ and ‘nurture’—as they went hand-in-hand with his anxiety about the decline of his race or nation—helped form the definition of heritability that is used today: the percentage of variance of a trait in a population due to inherited genetic factors (Keller 2010). Heritability is estimated by finding the association between observed phenotype and the variation due to genes as inferred by the degree of relatedness (Sultan et al. 2021). Plotting offspring trait values against their parents’ mean trait values yields a regression slope that estimates trait heritability (Sultan et al. 2021). While these estimates of heritability will include all inherited factors that may influence the resemblance between parents and offspring, these estimates are often interpreted based on an inaccurate, gene-centric, impression that heritability measures the “‘genetic contribution to a phenotype’ in a developmental, causal sense” (Sultan et al. 2021, 2). This suggests that Galton’s particulate notion of genetics and inheritance and his vision of the separability and opposability of nature and nurture has engrained itself in our understanding of

heredity that, in turn, may reveal a contributing factor leading to this second explanatory gap in gene-centric approaches to understanding inheritance (Keller 2010).

While GWAS can identify some of the genetic variants associated with certain phenotypic outcomes, these variants tend to be viewed as the only source of inheritance patterns. This assumption, however, is mistaken because researchers have observed that GWAS can only partially account for the parent-offspring resemblance, resulting in a phenomenon known as “missing heritability”: “the extent to which the evidently heritable portion of major trait variation is not explained by shared generic alleles” (Sultan et al. 2021, 2-3). In the case of human height, a familial trait with approximately 0.8 heritability, a statistically powerful GWAS of over 250,000 individuals identified 10,000 SNPs that additively contributed to height but only accounted for 36% of the heritability that was estimated based on observed variation patterns (Wood et al. 2014, cited in Sultan et al. 2021). Examples like this demonstrate the perplexing missing heritability phenomenon and point to the fact that “transmission of specific genetic variants fails to satisfyingly explain either the process or the phenotypic impact of biological inheritance” (Sultan et al. 2021, 2-3).

2.4.3 Explanatory Gap 3: The origins of novel, complex traits: Mutations are not the only source of evolutionary novelty

The third explanatory gap in gene-centric approaches is their tendency to rely on mutation as the source of evolutionary novelties. Out of the four evolutionary processes—natural selection, genetic drift, migration, and mutation—mutation is the only process that is afforded the ability to explain the origin of novel, complex traits, while the other three processes are limited to existing variants within and among populations (Sultan et al. 2021). While mutational variation has been important in identifying genetic variants that have contributed to novel trait

development, Sultan et al. assert that attempting to explain the origin of novel traits solely through the lens of mutation is limited because it cannot recognize how modularity and the context-responsiveness of development reveal that the self-regulating and self-developing nature of developmental systems are also an important source of innovative, evolutionarily-significant phenotypic variation (Sultan et al. 2021). This is not to say that mutation is not relevant or that mutation has not been significant in enabling sources of evolutionary novelty, such as modularity and trait integration, to take place in the first place. Indeed, systems' ability to reorganize its variation and produce complex and novel traits involves the evolution of new variants. Rather than discounting the importance of mutation in the origin of evolutionary novelty, the third explanatory gap attempts to reveal that mutation alone cannot account for these novelties because many of them arise through mutation *and* the resorting of existing variation.

Numerous complex traits known as evolutionary novelties evolved without the need to develop new genes, cell types, or pathways because phenotypic diversity can be instructed through the modular re-use and re-assembly of genes, developmental pathways, cell types, and morphogenetic processes (Sultan et al. 2021). This does not reduce the important role that mutation plays in creating the resources a system needs to modularly re-use and re-assemble standing genetic variation. Rather, the third explanatory gap attempts to highlight the ways that mutation serves as an important source of evolutionary novelty, but it is not the only source of novelty because developmental systems can *also* creatively leverage existing variation to produce novel traits. François Jacob articulates this paradox of the evolution of novelty (Kassen 2019) when he compares evolution to tinkering—"a tinkerer does not know exactly what [they] are going to produce but uses whatever [they] find around [themselves]...giv[ing] [their] materials unexpected functions to produce a new object" (Jacob 1977, 1163-1164). Similarly, "Evolution

does not produce novelties from scratch. It works on what already exists, either transforming a system to give it new functions or combining several systems to produce a more elaborate one” (Jacob 1977, 1164).

Insect wings, for example, are a morphological novelty, yet they develop from serially homologous¹² cell populations that are not only present in the wing segments, but also in the thorax, abdomen, and ancestrally-wingless crustaceans who share the same gene-regulatory network (Clark-Hachtel and Tomoyasu 2020, cited in Sultan et al. 2021). Additionally, many butterflies boast unique wing patterning that resemble eyes and aid in predator avoidance and mate signaling. Eyespot position, number, size, and color constructively emerge through a developmental pathway that is mostly independent from those regulating other wing-pattern elements (Brakefield et al. 1996). The evolution of these novel eyespot patterns can also occur quickly by modulating stages of the pathway, and involve only one, or minimal, changes in regulatory genes (Brakefield et al. 1996), demonstrating that evolutionary novelty is possible without the need to evolve novel genes, pathways, or cell types (Sultan et al. 2021). It is important to note that these examples would not have been able to take place without the help of mutation. I am not attempting to discount the important role that mutation plays in enabling the novelty in the previous examples, but rather demonstrate that developmental systems—due to their self-constructing, self-regulating, and self-adjusting nature—can also produce novelty by building off mutation’s work by rearranging and reassembling existing variation (Sultan et al. 2021).

¹² When two or more organs or structures share a similar construction but are modified to perform different functions.

Conclusion

These explanatory gaps of gene-centric approaches suggest that there are limitations to using component-to-system approaches to studying life. These limitations come from gene-centrism itself and the fact that its domain as an object theory is restricted to the study of objects, which comes with the need to make certain assumptions (causality) about the object of study based on the framework of the method (mechanism, reductionism) used to study it. These limitations do not indicate that gene-centrism is inherently flawed, but rather serve to point to the types of questions and contexts for which this approach is suited, and where it may benefit from a complementary way of studying organisms that is better suited to addressing context-specific dynamics that interrupt gene-centrism's supposedly one-to-one relationship between genotype and phenotype by introducing the space for plasticity, modularity, constructiveness adaptive responsiveness, developmental versatility, epigenetic, non-genetic bases for mutation and inheritance, and more.

Section 3

In the previous sections I explored some of the important developments in the history of science that have facilitated gene-centrism's rise to prominence as a strategy for studying organisms in biology. I also outlined intersections between paradigm and practice and experience and method in order to explore how the gene-centric perspective is shaped by our experiences with machines. For example, I explored some of the ways in which the gene-centric perspective relies on computational metaphors to describe organisms, which then reinforces a mechanistic perspective of life by informing how we learn about, conceptualize, ask questions about, and research organismal systems. I built off this discussion by outlining the benefits and limitations of a gene-centric framework, focusing on the features of the gene-centric framework and its perspective on organisms that may have facilitated its successes but also resulted in its three explanatory gaps and thus reveal a need for another approach—a biological agency perspective—that can overcome these limitations.

In this section, I introduce the biological agency perspective and explore the ways in which it overcomes gene-centrism's limitations. I begin by exploring the features of biological agency as an agent theory. Next, I compare biological agency as an agency theory to gene-centrism as an object theory in order to provide the necessary context for exploring some of the reasons why a biological agency perspective is better suited to the study of organisms. Finally, I complement Section 2.4's discussion of gene-centrism's three explanatory gaps by demonstrating that a biological agency perspective overcomes gene-centrism's limitations by addressing its three explanatory gaps.

3.1 What is agency and an agent theory?

While gene-centrism has been incredibly productive to biology and provides invaluable insights into mechanistic, context-insensitive dynamics, scholarship in philosophy of biology and biology identifies numerous explanatory gaps left when using a component-to-system approach to study organisms. These gaps are important because they reveal where gene-centrism reaches its limit when used to study organisms as objects of their genes' expression, and encourages both scientists and philosophers of science to consider the features of organisms that set them apart from nonliving objects reveals a need for a distinct theory and ontological category capable of accounting for living things as such. This category recognizes organisms as *agents* and takes into account an organism's *biological agency*—the “ways that organisms themselves actively shape their own structure and function” (Sultan et al. 2021, 4). Through their self-shaping activities, organisms also define, and help create and destroy their own niches; this phenomenon is known as “niche construction” (Odling-Smee et al. 1996) and it reveals the crucial fact that organisms not only adapt to their environment but, as agents, play a role in constructing them (Lewontin 1983). Agency is a measurable, observable phenomena, and it is also a metaphor that can help describe and organize complex systems in ways provide a scientifically viable complement to gene-centrism.

3.1.1 What is agency?

Agency refers to the capacity of a system to dynamically respond to changes in the conditions it encounters. While these conditions may change, an agent maintains functional stability by exerting influence over the activities of its component parts and on its external environment, which often results in the emergence of novel structures, functions, and activities (Sultan et al. 2021). Agents' adaptive responsiveness enables them to engage with the world, as

opposed to merely react to or be determined by it, in ways that support the agent's ability to sustain its persistence and vitality (Sultan et al. 201). Accommodating the conditions it encounters to maintain its persistence and continued vitality is a key feature of an agent's behavior, namely, its goal-directedness and purposiveness—responding to its environment and internal constitution in ways that enable it to pursue and maintain a goal state (Walsh 2015; Walsh 2018). Thus, agency is an “observable, predictable, explainable feature of the system's behavior” (Sultan et al. 2021).

Gene-centrism operates in the component-to-system (i.e., gene-to-organism), direction of explanation by studying systems and how they work in terms of their components parts. Biological agency complements gene-centrism because it operates in the system-to-component (i.e., organism¹³-to-gene) direction of explanation by showing how the dynamics of the organism's complex systems, and the organism itself in its particular context and through its

¹³ While I use the word “organism” here, the organism itself is only one example of a system that one might study using a biological agency approach. Other examples of systems might include the biology of the organism, such as all the parts of the nervous system as they work together, or the organism-environment relationship as captured by a specific niche within the environment that the organism has constructed through its activities. The important point to note about systems in the biological agency perspective is that the “system” in “system-to-component” is encompassing, coordinated, unifying, and relational; while components are isolated parts, a system is also made up of individual entities, but one could not isolate these parts to discern their causal role in the system as a whole because their interdependent co-functioning is what makes the system possible. Moreover, systems themselves are always made up of and embedded within other systems. For example, the nervous system includes many subsystems, each with a specific function that helps serve the system as a whole. The nervous system also functions in tandem with the brain, and the digestive, excretory, and endocrine systems, which themselves include innumerable layered yet connected subsystems, and it is a part of the body as a system which is further a part of that body's specific environment, which is also a system, and so on. The notion of systems within the biological agency perspective reveals relationality, inseparability in the sense that the parts of a system are interdependent and co-constitutive and therefore causally indistinguishable, and non-linearity. In doing so, the biological agency perspective is an approach that encourages biologists to consider parts not on their own but in terms of systems.

engagement with its environment, impact and shape the organism itself and the structure and activities of its genetic components (Figure 3.1).

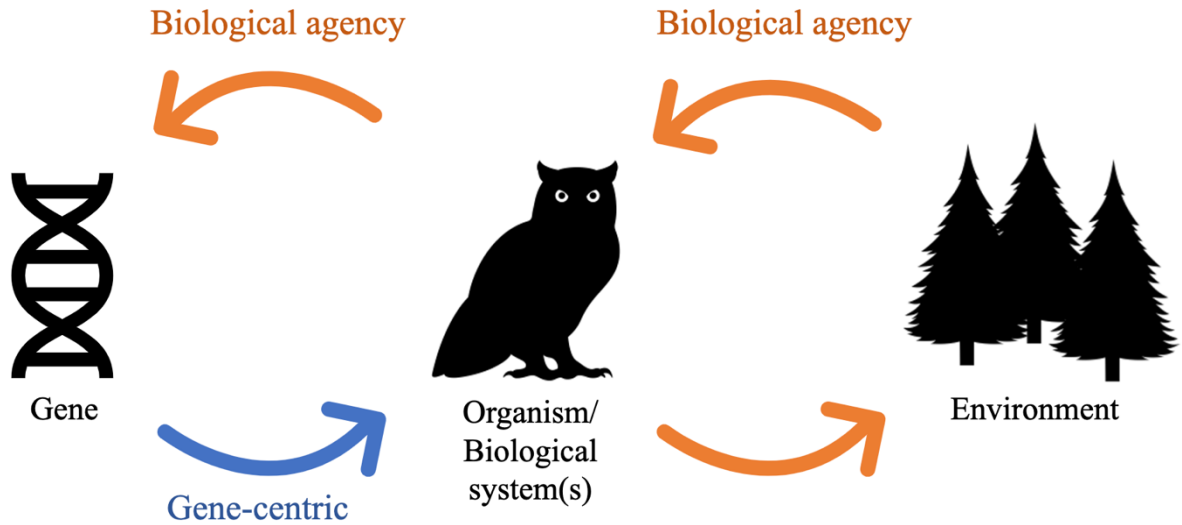


Figure 3.1: Representation of the component-to-system (gene-centric) perspective and its complementary system-to-component (biological agency) perspective.

The blue “gene-centric” arrow points in one direction from genes to organism, whereas the orange “biological agency” arrows are multidirectional and also connect the organism to the environment.

Figure adapted from Sultan et al. 2021.

The component-to-system direction of explanation highlights one of the defining features of biological agency is its ability to recognize organisms’ and their systems’ context-responsiveness and context- or environmental-sensitivity. For example, agency is observable in the context-responsiveness of “developmental, metabolic, immune, and endocrine processes” and “manifests in the adaptive plasticity of development and phenotypic accommodation—adjustments that modify the organism’s experience of environmental stresses—as well as the manipulation by organisms of their external environments in ways that facilitate normative development and maintain fitness (Sultan et al. 2021, 5). All of these processes rely on the organism being

embedded in and responsive to their environment, as opposed to able to exist in isolation from the environment like in context-insensitive gene-centric theories that explain processes by holding the external conditions constant. This suggests that biological agency recognizes that the organism's entanglement with its environment crucially shapes biological processes.

3.1.2 Object theories vs. agent theories

As the name suggests, biological agency is an *agent* theory. As we considered in Section 2, gene-centrism is an object theory because it operates in the component-to-system direction of explanation by using an organism's genes as the lens through which to explain biologically relevant processes like inheritance, development, and evolution. Object theories are characterized by what Walsh refers to as 'transcendence' and 'explanatory asymmetry' (Walsh 2018, 212). Walsh employs the word 'transcendence' to demonstrate that the principles governing the object of study in an object theory exist outside of that object as 'givens'; they are not part of the object's domain and they remain constant even as the object undergoes change (Walsh 2015; Walsh 2018). Accordingly, we can refer to these unchanging laws in order to study the object and how it changes because the principles themselves induce changes in the object, and not the other way around (Walsh 2015). The unidirectionality from genes to organism suggests that genes, though encased by the organism, exist in theoretical isolation from the organism as a whole because the changes in the organism itself cannot reciprocally induce changes in its genes (Figure 3.1). Furthermore, since object theories operate under the assumption that objects themselves cannot reciprocally explain the principles, object theories have an 'explanatory asymmetry' (Walsh 2015). In the case of gene-centrism, there is explanatory asymmetry in the linear and unidirectional relationship from genes (principles) to organism (object) because it assumes that the organism itself cannot reciprocally shape or be

used to explain its genes (Figure 3.1) The unidirectionality from genes to organism also demonstrates explanatory asymmetry because it implies that genes determine organisms and therefore hold the explanatory key to unlocking an understanding of organismal processes (Figure 3.1).

While object theories are characterized by transcendence' and 'explanatory asymmetry,' agent theories are characterized by 'immanence' and 'explanatory reciprocity' (Walsh 2015). An object theory is limited to the study of objects *as* objects of external principles (in this case, genes). However, the immanent nature of agent theories considers that agents engage with their environment. The agent, therefore, can be understood by appealing to the particular ways that it engages with its environment: "An agent's conditions and its capacities to act are immanent in the agent's engagement with its environment. The conditions that agents experience and their capacities to respond to them are interpenetrating and interdefining; each partially constitutes the other" (Walsh 2018, 176). In agent theories, agents can engage in and respond to conditions they encounter by endogenously altering their own conditions (Walsh 2015). Agents are also able to shape the conditions they may encounter and to which they may respond. This means that agents are able to enact response to conditions by both altering their state in response to the conditions and *reciprocally* transforming the conditions to which they respond (Walsh 2015). The dialecticality between agents and their conditions suggests that agents and their conditions are co-constitutive and therefore "each can be (partially) explained by appeal to the other" (Walsh 2015, 176). Accordingly, agent theories have explanatory reciprocity because both the "activities of the agent can be explained as a response to its conditions and, reciprocally, the change in conditions can be explained as a consequence of the activities of the agent" (Walsh 2018, 176). For example, while the gene-centric relationship between genes and the organism is

unidirectional, linear, and always begins with the genes, the relationship between genes and organism in the biological agency perspective is multidirectional, suggesting that their relationship is mutually co-constitutive as opposed to hierarchical or one-directional because the activities of the organism itself can reciprocally shape its genes, just as its genes are important in shaping the organism (Figure 3.1). Furthermore, unlike gene-centrism, the biological agency perspective also considers the dialectical relationship between the organism and its environment which represents the immanent organism-environment entanglement and reciprocity and reveals that the conditions the organism experiences and responds to are entangled with the organism itself (Figure 3.1).

3.1.3 What agency is not

Agency is not inherently an intellectual phenomenon. An agential system does not imply that the system has intentions, desires, or mindfulness (Keller 2005; Sultan et al. 2021). A human's cognitive and conative abilities are certainly expressions of agency, but these abilities are highly complex¹⁴ forms of agency that are not representative of the range of agential dynamics that qualify as agential but are not intellectual (Sultan et al. 2021). Agency also does not signify "providential design" (Sultan et al. 2021, 5). The most baseline form of agency exists in living systems, including unicellular organisms, that can adaptively respond to their conditions (Sultan et al. 2021).

In addition to not being an exclusively or inherently intellectual phenomenon, agency is also not a mechanical phenomenon. The dynamics of a machine can be understood by investigating the structure and functioning of its parts following the component-to-system mode

¹⁴ "Complex" in this sense is by no means meant to invoke a morally coded hierarchy of agency forms or indicate that intellectual expressions of agency are 'better' than nonintellectual forms.

of explanation (Sultan et al. 2021). The dynamics of an agent, however, necessitate the complementary system-to-component mode of explanation because their structure and activities cannot be exhaustively described by appeal to their parts' structures and activities.

Understanding why an agential system's components interact and have the functions that they do requires understanding how the agent as a system "regulates the properties and interactions of the components in pursuit of its goals" (Sultan et al. 2021, 5).

3.2 Why does the study of organisms need a biological agency perspective?

In the following subsections, I explore some of the reasons why organisms are crucially unlike machines in order to reveal their distinctive dynamics and processes that cannot be recognized through a gene-centric framework and therefore necessitate a biological agency perspective. I will demonstrate that one of the important characteristics that distinguishes organisms from machines is their context sensitivity and the interactivity between the organism itself, its environment, its genes, and its biology. This context sensitivity and interactivity illuminates that organisms are incredibly relationally embedded and dependent compared to machines, and therefore require a biological agency perspective that can recognize this distinctive feature.

3.2.1 Organisms are not machines

From Descartes to Dawkins, there has been a proclivity to compare living things to machines and their parts to the gears within them. As a student in the sciences, I am familiar with my professors using the metaphor of a blueprint or a code to describe genes and DNA. Gene-centrism, as a component-to-system approach, similarly relies on a machine model of the organism because it uses the organism's genetic parts in order to understand the system as a whole. Gene-centrism's analytic method of mechanistic decomposition also descends from the

Scientific Revolution's Cartesian doctrine *bêtes machines* and, as a part of this lineage, gene-centrism may be liable to reproducing its mechanistic legacy. For example, an entry in the *Encyclopedia of Neuroscience* defines clock genes¹⁵ as the “components of the circadian clock comparable to the cogwheels of a mechanical watch” (Urs and Jürgen 2009, 759-762). Many scientists and philosophers alike are critical of mechanistic comparisons like this; Talbott (2012) responds to the following entry about clock genes by saying that such a comparison “ought to be scandalous” (57). While reductionism and mechanistic decomposition have aided in the tremendous success of gene-centric approaches as I discussed in Section 2, Talbott's disapproval of comparing clock genes to cogwheels on a mechanical watch is a reminder that the limitations of gene-centric approaches are due, in part, to their tendency to rely on the misguided assumption that organisms are machines. In the following subsection, I will consider some of the reasons why organisms are not machines, and why this suggests the need for a biological agency approach that can account for the nuances of organismal life that sets them apart from machines.

Across all sciences are ‘what for?’ questions that inquire into the functions of parts and processes (Lewontin 2000, 81). In biology, however, asking ‘what for?’ is entirely different than if one were to ask the same question while analyzing the parts of a car or a clock (Lewontin 2000). In the case of cars and clocks, an object theory like the analytic method would be relevant for an investigation into the ‘what for’ question because both cars and clocks are nonliving objects and can be understood in terms of their parts.¹⁶ Following that object theories are

¹⁵ Clock genes provide information for the clock proteins. The activity between clock genes and clock proteins, in conjunction with external cues like light and darkness, help regulate the body's circadian rhythms.

¹⁶ One might argue that there are certain machines, or, nonliving objects, such as Artificial Intelligence, that can be goal-directed and therefore evaluated using an agent theory as opposed to an object theory to appeal to this capacity. It might be worthwhile to explore nonliving objects that exhibit goal-directedness, but agency in the context of my thesis refers not only to entities

characterized by transcendence and explanatory asymmetry, one could inquire into the ‘what for?’ of the car and the clock by assuming that there are certain functions, all of which are known in advance, that each part within each object is meant to fill (Lewontin 2000). Organisms certainly have common functions that are known in advance—respiration, reproduction, motion—but, unlike machines, there are unique functions that cannot be known in advance or expected as ‘givens’ (Lewontin 2000). In some cases, there are parts that may not serve functions at all (Lewontin 2000). Since organisms are unlike machines in this way, the functions of an organism’s genetic constituents cannot be answered without recognizing the “dialectical relation between parts and wholes”; accordingly, “Before we can recognize the meaningful parts, we must define the functional whole of which they are the constituents” (Lewontin 2000, 82). Through its emphasis on immanence and explanatory reciprocity, biological agency accounts for an organism’s genetic parts and processes by recognizing the organism itself and the ways in which its activity in and engagement with the world influences and co-determines the workings of its parts.

Moreover, unlike machines—which can be explained by reconstructing the relations among their parts—the dialecticality between parts and wholes in an organism often results in the parts in question changing from moment to moment, and their significance or function

with goals, but entities whose goals are set *internally* (Keller 2005). That being said, even if there are certain machines that can be goal-directed, this does not mean that machines are organisms, or that goal-directedness is the necessary and sufficient condition to qualify something as an organism. One of the reasons for this lies in the distinction between organisms and machines: while machines are designed and directed towards goals from without, organisms’ organization and goal-directedness is internally generated (Keller 2005). I would imagine that elements of this machine-organism distinction came into play in the coining of the term “biological agency” to clarify that there is a unique form of agency that applies to biological, or *living*, systems and not machines. In this section, I explore some of the notable dynamics that set organisms apart from machines, and even goal-directed machines, and necessitates the biological agency perspective.

adaptively changing from context to context (Talbot 2012). Consider a simple definition of a gene as a sequence of DNA nucleotides that codes for a protein. This sequence of nucleotides does not do anything alone. It has no power to ‘act’ by ‘causing’ the development of characters or traits; it is an inert molecule (Keller 2010). Whatever one does define as a gene is so fundamentally woven into the cellular processes and relationships of which it is a part that any identity and function that one could attribute to the individual gene cannot be separated from whatever context from which it is a part (Talbot 2012). What one would consider the gene’s ‘causal powers’ to act are given by the cellular complex in which it is located (Keller 2010). Similarly, the molecular networks within which a particular gene is embedded is nested within layers of other contexts, extending ‘outside’ of the organism itself to its environment, that too change from moment to moment. Much like the sequence of nucleotides depends on the cellular complex of which it is a part, this same gene cannot be considered in isolation from the surrounding molecular, cellular, or otherwise surrounding intraorganismal environment, or environment in which the organism is located because patterns of gene expression are bound up in a complex of compounding interactions between intra- and extraorganismal environmental stimuli and the DNA molecule’s structure, conformation, and nucleotide sequence (Keller 2010). The interactive nature of organismal systems and their contextual sensitivity further challenges the machine model of the organism because it reveals that its relations between parts are not linear and unidirectional, but reciprocal, making it incredibly difficult (and, in some cases, irrelevant) to try to discern causes from effects. Lewontin summarizes this idea when he states that “the relations of genes, organisms, and environments are reciprocal relations in which all three elements are both causes and effects. Genes and environment are both causes of organisms,

which are, in turn, causes of environments, so that genes become causes of environments as mediated by the organisms” (Lewontin 2000, 100).

Another reason why organisms are unlike machines that suggests the need for a biological agency approach is that organisms grow out of themselves with an internal unity from the very beginning (Talbot 2012). By this, I mean that the parts of an organism grow out of the organism itself or become incorporated by the organism; “They do not add themselves together to form a whole, but rather progressively differentiate themselves out of prior wholeness of seed or germ. They are growing even as they begin functioning, and their functioning is a contribution toward their growing. The parts never were and never are completely separate, never are assembled” (Talbot 2012, 56). Machines, on the other hand, are designed and assembled from without (Keller 2005). The concept of design is still relevant for organisms, but this design, this organization, is “internally generated” (Keller 2005).

3.2.2 Interconnected and interactive embeddedness of genes, biology, organisms, and their environment reveals relationality as opposed to isolated factors and linear causality

In the previous subsection I explored some of the reasons why organisms are crucially unlike machines. For example, while machines can be explained by appealing to the structure and functioning of its parts, the “parts” of an organism are context sensitive such that their role and function cannot be understood without considering the system(s) of which they are a part. One of the other factors I have considered that distinguishes organisms from machines is the interconnected and interactive embeddedness of genes, organismal systems, and the organism’s environment. Organisms are certainly formed, in part, by their genetics, but an organism’s genes cannot be equated to a machine’s parts or gears because organisms are not passive objects of

their genes' predeterminations, but agents that enact and mutually shape their genes' expression. While there is a linear and unidirectional relationship from gears to machine, this is not the case for the relationship between genes and organisms because organisms are constantly accommodating layers of interactions across many levels, from the genetic and molecular level to the environment(s) in which it lives. Considering some of these factors that set organisms apart from machines is important because it reveals that organisms' agential dynamics rely on relationality and interactivity between and among organismal systems and the organism's environment. Accordingly, organisms need a biological agency approach that can recognize that their dynamics are relationally-sensitive and interactive, rather than unidirectional, mechanistic, or context-insensitive.

Considering the relational dialecticality between the parts and wholes of an organism reveals that the organism is not necessarily an aggregate of discrete components, but rather a system with innumerable entangled and embedded subsystems of which the 'parts' are not like gears but like interactive *members*.¹⁷ Recognizing this relationality and interactivity between not only the organism and its environment, but between and within systems and members within an organism more adequately represents organismal dynamics. Take, for example, the signaling pathways within an organism. These pathways are crucial means of communication within and between cells (Talbot 2012). "In the machine model of the organism, such pathways were straightforward, with a clear-cut input at the start of the pathway leading to an equally clear-cut

¹⁷ Throughout this thesis, I have explored the ways in which words carry meaning, especially when used metaphorically to describe a scientific concept. Following this consideration, I believe it is worthwhile to introduce the idea of "members" as an alternative to the word "parts" to describe organismal systems specifically and set them apart from machines. The word "member" is similar to the word "part" in that they both imply being a part of something larger. However, "part" suggests a mechanical and rigid relationship whereas "member" implies a more organic, living, and interactive relationship.

output at the end” (Talbot 2012, 52). In this depiction of signaling pathways, the parts are related to one another, but their relationship is mechanistic and linear, rather than interactive. A team of molecular biologists, however, discovered that signaling pathways are interactive and relational in a way that is neither mechanistic nor linear (Dumont et al. 20001; Talbot 2012). Upon closer examination of four signaling pathways, the biologists found that these pathways “interact or ‘crosstalk’ with one another. Tabulating the cross-signalings among just four such pathways yielded what they called a ‘horror graph,’ and quickly it began to look as though ‘everything does everything to everything.’ In reality, we see a ‘collaborative’ process that can be ‘pictured as a table around which decision-makers debate a question and respond collectively to information put to them” (Dumont et al. 2001, quoted in Talbot 2012, 52). This example demonstrates that the parts of an organism are not necessarily linked mechanistically or linearly; rather, the cross-talking, dialectical relationship between members suggests that their relationship is entangled and much harder to causally discern due to its interactivity.¹⁸

¹⁸ It is worth mentioning that Dumont et al.’s (2001) depiction of the signaling pathways’ interactivity, like the machine model of the organism, relies on metaphorical or otherwise figurative language. As I have previously explored, there can be slippages and misinterpretations that come with using figurative language to describe biological processes. For example, the metaphor that a gene is a code might misdirect one into overestimating a gene’s causal power to create phenotypes. Similarly, Dumont et al.’s use of personified language to describe signaling pathways might be misleading because it anthropomorphizes the members of the signaling pathway and figuratively suggests their intentionality. That being said, as a reader, did you notice any difference in the effect of Dumont et al.’s figurative language on how you imagined the biological process compared to the computational and mechanistic figurative language of the machine model? Personally, Dumont et al.’s depiction of the signaling pathways’ dynamics invoke *living* imagery, while the metaphors that come with the machine model invoke much more machine-like visualizations. I point this out because it demonstrates that the language we use to describe biological processes shapes how we understand, study, and ask questions about life. Accordingly, when attempting to portray biological—*living*—systems and processes, metaphors that draw from our experiences with life, of life, and of being alive may be more appropriate than metaphors that draw on our experiences with machines.

In their description of signaling pathways, Dumont et al. (2001) do not mention that the members of the pathways themselves are not only interacting with one another, but are also taking cues from and responding to information from neighboring intraorganismal systems and the extraorganismal environment. The interactive and interconnected relationships among signaling pathways members and between them and other systems and environments is an example through which to see that the members of biological systems are neither discrete nor necessarily isolatable but find their meaning in their particular context as it emerges by and through interactions and context-sensitive relationships. Since biological systems and members emerge out of a particular context and from a network of interconnected and embedded interactions, this suggests that biological boundaries—boundaries between members and systems, systems and systems, systems within and the organism as a whole, or between the organism and its environment, for example—are not rigid but porous and flexible. Lewontin asserts that this openness is a key feature that distinguishes living systems from physical ones; he writes, “the characteristic exchange that occurs between the inside and the outside [and]... The softness of the boundary between inside and outside is a universal characteristic of living systems” (Lewontin 2000, 125). The flexible and porous boundary between organismal systems and between the organism and its environment reiterates the idea that organismal members and systems are neither discrete parts nor linked mechanically, but contextually accommodating and relationally sensitive.

3.3 A biological agency approach overcomes the limitations of gene-centrism by providing a complementary approach to studying organisms

3.3.1 Addressing Gap 1: Phenotypes are not fixed, but responsive

Gene-centrism, as an object theory, is an abstraction¹⁹ of the genetic-environmental factors (Keller 2010) that dialectically and co-constitutively shape the organism's development. This is because gene-centrism, operating in the component-to-system direction of explanation, cannot account for the way in which the system as a whole and its engagement with its particular context reciprocally shapes its genes, and because, in adopting the mechanistic analytic tradition, mistakenly assumes that an organism's development of certain traits can be portrayed in terms of "separable causes" or as "product of causal elements interacting with one another" (Keller 2010, 6). In fact, the multiplicity of causal elements coming from both the organism's environment and its genes is too complex to even describe as "interacting" or "intersecting" because this supposes an a priori space between component entities (Keller 2010). In reality, the processes of inheritance and development are entangled:

From its very beginning, development depends on the complex orchestration of multiple courses of action that involve interactions among many different kinds of

¹⁹ The etymology of the word 'abstract' comes from the Latin *abstractus*, which signifies something that has been 'pulled out' or 'drawn away.' It is the past participle of the word *abstrahere*—*ab-* meaning 'from' and *trahere* meaning 'draw off'—indicating that the action of 'drawing off' has already been completed. This suggests that an abstraction has a static quality because, in reducing the complexity of something to a single signifier, pulls the thing out of its context. In this context, I use the word abstract in the way that Hegel uses it in his essay "Who Thinks Abstractly?" to signify that which has been taken out of its original context; in this case, gene-centrism is a multidimensional abstraction. It is an abstraction of the organism because it considers it in isolation from its environmental context. It is an abstraction of the genes themselves because it assumes genes are discrete, causal entities. And, even if genes were causal units (which they are not), gene-centrism, in its most mechanistic form, further abstracts genes from genes by assuming they can operate independently from one another, when even causal components are always components of *something* and therefore need some sort of relationship to operate even in a mechanism (Keller 2010).

elements—including not only preexisting elements (e.g., molecules) but also new elements (e.g., coding sequences) that are formed out of such interactions, temporal sequences of events, dynamical interactions, etc., compounding the entanglement between genes and environment yet further. (Keller 2010, 6-7)

If development is not only environmentally sensitive but also the synthesis of genetic-environmental factors, it is reasonable to expect that a gene-centric approach would be limited in its ability to reliably explain the process or the phenotypic impact of biological inheritance or discern disease causality, for example. The causal claims deduced through object theories like gene-centrism typically assume context insensitivity and that all conditions remain constant, but in biology this is almost never the case (Lewontin 2000).

One of the characteristics of a living being, according to Lewontin, is that it “reacts²⁰ to external stimuli rather than being passively propelled by them” (Lewontin 2000, 93). While matter is passively acted on and reacts according to the properties of its material constituents, as expected of objects within object theories, Lewontin suggests that one of the defining features of organisms as distinctly different from nonliving objects is their ability to exhibit a more active, and perhaps unpredictable, response to external stimuli. If one pushed a ball with the right amount of force, the ball would react by rolling away, as one would probably expect; but if one pushed a person, they would probably push back. This example is incredibly simple, but it serves to demonstrate the idea that organisms do not just react to external stimuli based on a set of universal laws but enact responses. However, as I have previously discussed, gene-centrism and its component-to-system method is an object theory, and therefore cannot account for how an organism may respond to external stimuli in ways that are not predictable based solely on its

²⁰ I prefer to use the word *respond* in place of Lewontin’s use of the word “react” because it moves away from physiochemical language that invokes the image of particles colliding during a chemical reaction and instead characterizes organisms’ “reaction” to external stimuli as uniquely active and organic.

genetic components. In fact, gene expression can be flexible, resulting in environmentally contingent or *plastic* phenotypic outcomes²¹ in development, physiology, life-history, and behavior in all living systems (Sultan et al. 2021). Many of these plastic outcomes are suited to the unique conditions that brought them about, offering a form of adaptation at the individual level (Sultan et al. 2021). Since plastic responses are elicited when an organism senses an environmental change that informs its phenotypic expression, plastic outcomes are characterizable, repeatable, and unique to the eliciting conditions (Sultan 2015). The relevance of plasticity to organisms' phenotypic outcomes further illuminates the responsive nature of organismal life. It also suggests that one of the reasons gene-centric approaches are limited in their ability to explain phenotypic differences from a genetic basis might be due to a misguided assumption inherited from the gene-centric framework as an object theory that gene expression is rigid and environmentally-insensitive, and organisms are passive objects of their genes' expression. A biological agency perspective, however, focuses on organisms' dynamic processes and environmental sensitivity rather than on genes alone. This creates the opportunity to recognize the fact that organisms' context-dependency and environmental responsiveness

²¹ *Phenotypic plasticity* is condition-sensitive development or an organism's ability to respond to an environmental input with a change in "form, state, movement, or rate of activity" (West-Eberhard 2003, 34). West-Eberhard (2003) uses the words "responsiveness," "flexibility," "malleability," "deformability" and "developmental plasticity" as synonyms for her definition of phenotypic plasticity, which I am also doing (35). *Phenotypic plasticity* is also the ability of a given genotype to produce varied phenotypes in response to distinct environmental conditions (Pigliucci 2001). Plasticity is intra-individual variation in the sense that variation in environmental conditions an individual experiences can produce a range of phenotypes given their genotype (Evans 1953; G. C. Williams 1992, cited in West-Eberhard 2003). Defining plasticity as intra-individual variation illuminates the interplay and dual influence of environment and genes, for "intra-individual variation during development is obviously the result of inputs from both sources, with the individual's genome a constant and its environments responsible for variation in its phenotype over time or topography" (West-Eberhard 2003, 34).

“mediates between genes and the development of phenotypes” (Sultan et al. 2021, 4), as is the case for plastic phenotypic outcomes.

The pathways that underscore plastic expression patterns can be generally referred to as *cue and response systems*: “developmental, physiological, or behavioral adjustments (whether adaptive or maladaptive) that occur when an organism *perceives* some aspect of its environment as a specific piece of information and then *responds* to that cue by expressing particular phenotypic effects” (Sultan 2015, 49). Unlike component-to-system approaches to studying organisms, cue and response systems are not singular, linear pathways but overlapping networks that integrate feedbacks of genetic and environmental cues throughout the organism’s life cycle. Phenotypic outcomes reflect the integration of these entangled cues through plastic trait expression. Accordingly, cue and response systems comprise the “signal transduction networks that are embedded in larger regulatory networks” (Sultan 2015, 49).

Phenotypic plasticity suggests that genes and the environment operate as a synthesis of processes, to which the organism is actively sensitive and responsive, helping shape phenotypic outcomes. Accordingly, plasticity dismantles the genetic determinist assumption (Figure 2.1, Figure 2.2) that genotype space and phenotype space are discrete, with the former being the more important of the two,²² because it helps reveal the way that organisms’ development is not genetically determined but made up of “dynamically reciprocal pathways in which gene activity

²² This issue of the separation and the creation of a hierarchy between genotype and phenotype and genes and environment descends from the assumptions of object theories and the implicit separation and opposing of “nature” (genetic) and “nurture” (environment). This suggests the importance of examining the assumptions implicit in the frameworks used in order to see how research questions and methods may be predisposed to gene-centric limitations, such as those identified in Sultan et al. 2021. Exploring the limitations of the gene-centric framework in this way may preemptively avoid developing studies that result in explanatory gaps that may have been anticipated by examining the limitations of a component-to-system approach.

both shapes and is shaped by the organism's regulatory developmental and functional processes" (Sultan et al. 2021, 4). Understanding phenotypic development and variation therefore requires attending to these dynamically reciprocal pathways by considering not only the organism's genes, but the myriad of environmental cues to which the organism and its biology may respond to depending on its particular sensory apparatus and environmental sampling abilities and behaviors (Sultan 2015, 52). For example, numerous fish species have the ability to remodel their gill structure in response to environmental cues such as temperature and oxygen levels (Sollid and Nilsson 2006, cited in Sultan et al. 2021). The crucian carp (*Carassius carassius*) and goldfish (*Carassius auratus*) are dramatic examples of fish gill plasticity; in hypoxic or high temperature conditions, gill surface area increases in individuals to withstand these conditions (Sollid and Nilsson 2006, cited in Sultan et al. 2021).

The organism's ability to accommodate and respond dynamically to reciprocal causal pathways invokes additional characteristics of living organisms, namely, their correctiveness and internal heterogeneity, that make it impossible to deterministically predict phenotypic outcomes or derive causal claims about processes like inheritance or development:

An organism's life consists of constant mid-course corrections. Organisms are also extremely internally heterogeneous. Their states and motions are consequences of many intersecting causal pathways, and it is unusual that normal variation in any one of these pathways has a strong effect on the outcome....The multiplicity of causal chains, all of weak individual influence in their normal condition, presents a special difficulty for the attempt to understand life processes. (Lewontin, *The Triple Helix*, 93-94)

The multiplicity of weak intersecting causal chains and the organism's correctiveness that Lewontin articulates are features of plasticity, reiterating the need for a complementary biological agency approach that can recognize how gene activity influences and is influenced by organisms' precise environmental sensitivity. For example, environmental cues are commonly made up of numerous interacting elements that are partly redundant in order to ensure

environments are accurately sensed and that responses are robust and carefully calibrated (Sultan 2015, 54). These responses are frequently characterized by overlapping, combinational cues (Sultan 2015, 54). For instance, leaves' stomatal behavior, essential for regulating the plant's carbon fixation and water loss, is made up of many interacting environmental cues. The opening and closing of the stomata on plants' leaves is the result of a balancing of extra- and intracellular environmental inputs, such as light (notably blue light), carbon dioxide concentration, water vapor pressure, fluxes and movement of ions, sugars, and hormones (Sultan 2015, 54-55). These regulatory pathways have yet to be completely elucidated, but it is known that the orchestration of stomatal behavior draws from numerous simultaneous and partly redundant signals, feedbacks, and chemical signaling parts that also play a role in other cellular processes (Sultan 2015, 55). This network of interactions challenges the gene-centric assumption of a linear topography of isolated, 'stand-alone' pathways by illuminating the interconnectedness of signals that further enables both a robustness to loss of certain member signals and an ability to balance multiple cues (Sultan 2015, 55). The integrative and sensitive nature of stomatal regulation is further evidenced by plants that have been repeatedly exposed to environmental states, such as high carbon dioxide levels, demonstrate different sensitive responses to *other* signals, such as drought or abscisic acid, compared to plants that were not exposed to these conditions (Casson and Hetherington 2010, cited in Sultan 2015, 55).

A biological agency approach can complement a gene-centric approach to understanding phenotypic development and variation because it is suited for the consideration of environmentally sensitive processes. Research focused on these processes has the possibility of providing important new causal insights (Sultan et al. 2021, 6) because it can recognize how the organism is sensitive to environmental information and that this information can produce a range

of phenotypic response mechanisms that would have gone overlooked by a gene-centric approach. For example, the squid *Euprymna scolopes* and its microbial symbionts, the luminous bacterium *Vibrio fischeri* engage in a complex “host-symbiont dialogue” (McFall-Ngai 2014, 9). The bio-chemical cues that *E.scolopes* receives from *V. fischeri* directly drive the squid’s circadian rhythms, maturation processes and timing of developmental changes, behavioral strategies (e.g., helps produce light to support the squid’s antipredatory camouflage), among other processes, evidencing the need to consider not just genes in order to understand the nuances of animal development and behavior (McFall-Ngai 2014). Similarly, biomedical researchers are examining the connection between risk of inflammatory disease and the composition of a child’s lung and gut microbiomes in order to understand asthma development (Rivas et al. 2016, cited in Sultan et al., 2021). These microbiomes modulate the immune system’s development and function and are themselves shaped by post-natal environmental conditions, potentially suggesting these microbiomes may be responsive to therapeutic intervention (Rivas et al. 2016). Research like this that focuses on an organism’s dynamic processes, in conjunction with a gene-centric approach, can help illuminate the network of interactions mediating the not-so-linear space between genotypes and phenotypes. This may offer a more nuanced understanding of biological causality and its relationship to phenotypic outcomes which, in turn, may expose new therapeutic targets and interventions (Sultan et al. 2021).

3.3.2 Addressing Gap 2: Norms of reaction

While the Mendelian model situates heredity as the simple transmission of the DNA sequence, research examining the effect of parent-environment interactions, cytoplasmic factors, and epigenetic transmission has revealed that the process of biological inheritance is much more

nuanced and environmentally constructed (Sultan et al. 2021). The point that is important to recognize here is that genes themselves are environmentally shaped entities, so parents passing their genes to their offspring is not simply genetic inheritance, but environmental inheritance. For example, molecular epigenetic mechanisms (e.g., DNA methylation, small noncoding RNAs, and histone modifications), as well as cytoplasmic cellular components and non-DNA bound factors such as hormones induced in response to environmental conditions may shape parental genotypes (Sultan et al. 2021). Many of these parent-environment interactions are heritable, demonstrating that environmentally induced changes to parental genotypes can affect offspring development in ways that are both ecologically and evolutionarily relevant (Adrian-Kalchhauser et al. 2020; Sultan et al. 2021). These parent-environment mechanisms and effects are not uniform across the genome and in different taxa (Adrian-Kalchhauser et al. 2020) and the developmental impact of parent-environment interactions varies depending on the offspring's environment (Sultan et al. 2021).

These parent-environment effects and epigenetic transmission demonstrate that the Mendelian model of heredity as simply the transmission of the DNA sequence offers an insufficient account of biological inheritance and the development of specific phenotypes. This model of inheritance aligns with the determinist, component-to-system assumption that genes are context-insensitive entities because it does not account for the fact that genes are environmentally responsive. Development is not the conditional execution of a genetically determined phenotypic script, but rather an organic response drawing from the fundamentally interactive effects of genetic and environmentally shaped regulatory information, including epigenetic and cytoplasmic factors, many of which are heritable and will go on to influence phenotypic expression in offspring (Adrian-Kalchhauser et al. 2020; Sultan et al. 2021). This

serves to demonstrate the fact that organisms are crucially shaped by their environment and go on to pass their environmentally shaped genotypes onto their offspring. Accordingly, biological inheritance can be more adequately understood by taking into account organisms' capacity to “modulate and transmit phenotypic information to their descendants, and better understanding how those descendant individuals draw on this information in their own genetic and environmental contexts” (Sultan et al. 2021, 6).

The importance of environmental inheritance leads to the point that the range of phenotypic responses of a single genotype to a range of environmental conditions—that is, its *norm of reaction* (Figure 3.2)—is not a deterministic, predictable, execution of the information encoded in its genes, but a dynamic response that integrates various entangled genetic and environmental inputs inherited from their parents' environments (Sultan et al. 2021).

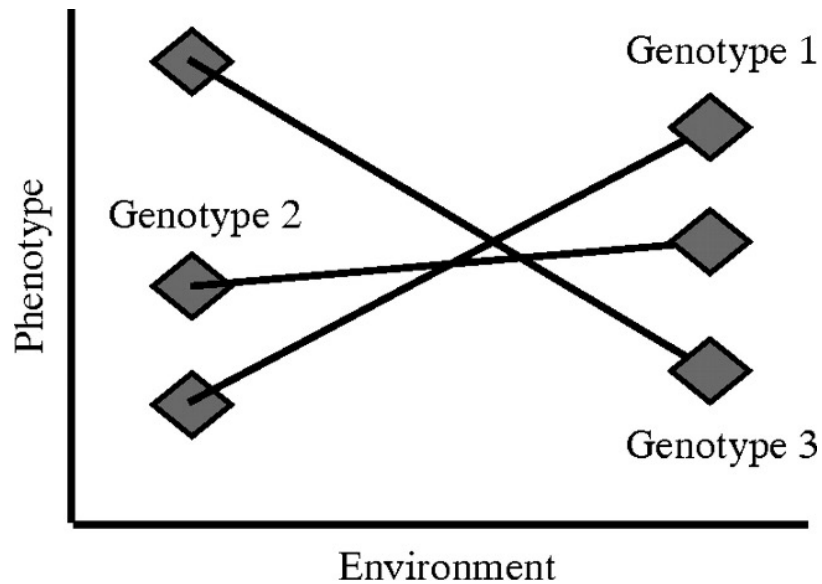


Figure 3.2: Example of genotypic reaction norms to visualize phenotypic plasticity.

Considering a simplified example of two environments, the lines represent each genotype's norms of reaction, while the slopes estimate the degree and pattern (positive or negative of phenotypic plasticity). For example, genotype 1 demonstrates a positive plastic response to the environment, but in this same environment, genotype 3 exhibits the opposite pattern of plastic response.

Genotype 2 demonstrates minimal phenotypic plasticity for this environment compared to genotype 1 and genotype 3. Figure from and figure caption adapted from Pigliucci et al. 2006.

In his experiments with fruit flies (*Drosophila melanogaster*), Waddington (1953) conducted some of the earliest work demonstrating the concept of norms of reaction. Waddington found that certain phenotypes—such as the cross-veinless phenotype in *Drosophila*—can be induced at low frequencies in a population by environmental stimulus—such as certain stresses like heat shock at certain developmental stages (Pigliucci et al. 2006). Waddington selected for flies with the cross-veinless phenotype to increase the frequency of the plastic phenotype in the population. After only a few generations of experimentally induced selection, Waddington observed two effects: the frequency of the plastic phenotype increased in the population and, more surprisingly, the environmental stimulus no longer seemed required to induce the cross-veinless

phenotype (Pigliucci et al. 2006). Waddington discussed his observation of the inheritance of an acquired character, known as assimilation, in terms of the canalization of the phenotype; the inheritance of an acquired character was followed by selection for adaptive responses to the environmental stimulus, and finally stabilization of the reaction norm (Pigliucci et al. 2006) (Figure 3.3).

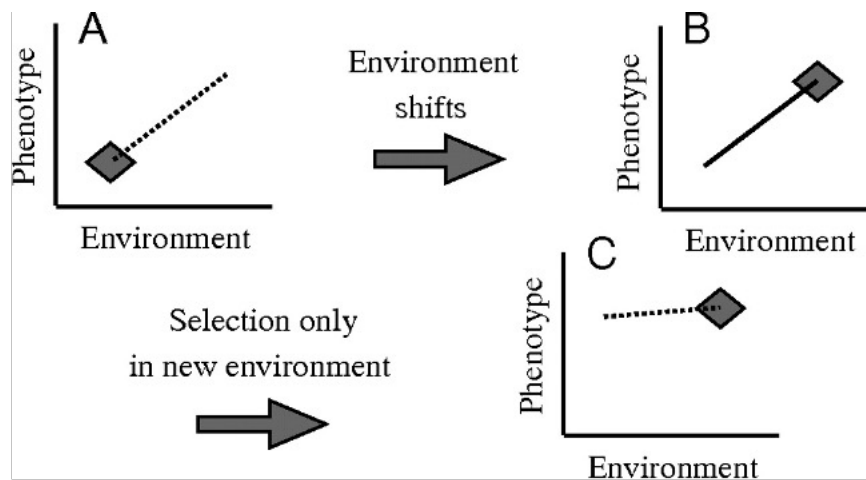


Figure 3.3: Representation of genetic assimilation in the context of reaction norms and phenotypic plasticity.

The population begins by occupying environment A, but the reaction norm indicates that the population has the ability to exhibit phenotypic plasticity if the environment were to change. If the environment shifts (B), then the reaction norm from environment A allows the population to persist by producing a novel phenotype without any initial genetic changes. If natural selection keeps operating only in the new environment (C), then the novel phenotype may become genetically fixed (assimilated). The assimilation of the novel phenotype in the new environment (C) may cause the original reaction norm to lose plasticity because the old environment is no longer being experienced Figure from and figure caption adapted from Pigliucci et al. 2006.

Waddington’s observations were some of the first to exemplify the fact that “phenotypic plasticity is a common property of the reaction norm of a genotype (for a given trait, within a certain range of environmental conditions). Plasticity is what makes possible the appearance of an environmentally induced novel phenotype” (Pigliucci et al. 2006, 2363). This example serves

to demonstrate that genes are not the ultimate difference-makers in development; rather, “genes are followers” shaped by the organism’s environment (West-Eberhard 2003, 20). This serves to demonstrate that biological inheritance is not the passing-down of genes as predetermined DNA codes, but the passing down of genes as shaped by previous environments (Nishikawa and Kinjo 2018).

Norms of reaction suggest that an individual’s genotype has a phenotypic repertoire, or a “wide range of outputs that it can produce across a range of circumstances” that is largely dependent on the developmental system’s regulatory influence (Walsh 2015, 124). Accordingly, “it is the norms of reaction that are the proper object of study for developmental biologists rather than some ideal organism that is supposed to be produced deterministically from the genes” (Levins and Lewontin 1985, 94). Rather than studying organisms as the object of its genes, which not only objectifies the organism but dilutes and linearizes the network of relationships that organically co-constitute the organism, the organism’s norm of reaction illuminates the network of processes at play in forming the organism and encourages the reconciliation, as opposed to the reduction, of these gene-environment-organism relationships involved in organismal development. Accordingly, a biological agency perspective of inheritance may be able to overcome the inheritance gap left by gene-centric approaches by “identifying the capacities of organisms to modulate and transmit phenotypic information to their descendants” as well as clarifying how those offspring leverage this information in their own genetic and environmental contexts (Sultan et al. 2021, 6).

3.3.3 Addressing Gap 3: Novel traits emerge through mutations, but also because of the organism's modularity, trait integration, constructiveness, and robustness

The third explanatory gap left by gene-focused approaches that Sultan, Moczek, and Walsh (2021) identify regards the origin of novel traits. While mutations in existing genes and regulatory elements are certainly important in the origin of novel, complex traits, new mutations, by themselves, are not entirely capable of explaining why, how, and when evolutionary novelty unravels the way that it does. This does not mean that mutations are not involved in the evolution of novelties; rather, it suggests that evolutionary novelty is also possible without the need to evolve novel genes, pathways, or cell types, with mutation likely playing an important role in reorganizing ancestral development structures.

For example, organismal development is a modular process whereby phenotypic variation emerges through the context-sensitive configuration and reconfiguration of existing components and processes (Gerhard and Kirschner, 2007; Sultan et al. 2022). Modularity, or discreteness, is a fundamental, emergent feature of organisms and complex systems whereby its component modules, which have local and independent genetic and developmental control yet are highly coordinated, can be disassembled and rearranged into new formations in response to genomic or environmental inputs in order to achieve multiple functions (Felice et al. 2019; Mitteroecker 2009; West-Eberhard 2019; Zelditch and Goswami 2020). Organisms' modular design has been recognized for promoting diversity because rearranging preexisting atomical 'units' can more efficiently expand ecological diversity than the independent evolution of each part (Hu and Albertson 2021). Exploring patterns of modularity may broaden the explanation of the novel traits that has eluded quantitative and population genetic approaches because patterns of modularity may limit or facilitate the evolution of phenotypic diversity by impacting the

arrangement of variation on which selection may act (Felice et al. 2019; Zelditch and Goswami 2020). In addition to modularity, organismal development is also a very constructive process whereby aspects involved in the formation of phenotypes build upon previously formed and developed phenotypes (Gerhard and Kirschner 2007; Sultan et al. 2021).

Modularity, constructiveness, and context-responsiveness are important factors in the evolution of phenotypic disparity because they facilitate trait integration, robustness, and adaptability (Felice et al. 2019; Gerhard and Kirschner 2007; Sultan et al. 2021). Trait integration, as well as phenotypic integration and morphological integration, denotes the relationships and patterns of correlation between and among numerous components within a module in a complex phenotype and their relationships to other modules in the organism (Murren, 2012; Zelditch and Goswami, 2020). Modularity facilitates trait integration by describing the degree to which highly integrated traits can form quasi-independent units that can remain functionally and/or developmentally interdependent so as to produce an organized organism (Murren 2012). Cichlid fishes in the family *Cichlidae*, for example, exhibit incredible diversity among vertebrates (Kocher 2004) and are well known for the extent and speed at which they diversify (Hu and Albertson 2021). Research on cichlid fishes has revealed that these fishes demonstrate integration and modularity at the genetic, anatomical, functional, and evolutionary levels, and especially with regards to the skull, which may promote the origins and continuation of cichlids' incredible diversity and unparalleled evolutionary success (Hu and Albertson 2021). One example of cichlid modularity is at the functional level, whereby distinct anatomical units play distinct roles: while the cichlid oral jaw is involved in the action of prey capture, the pharyngeal jaw is involved in prey processing (Hu and Albertson 2021). This specialized innovation is one of many that has been credited for cichlids' evolutionary success in terms of

cichlid eco-morphological diversification (Hu and Albertson 2021) because it allows cichlids to carry and process food and enables the premaxillary and mandibular jaws to evolve various specializations that can aid in the collection of a wide array of prey types (Liem 1973).

Modularity and context-responsiveness also enable organisms to display a great deal of robustness and adaptability. Robustness means that a system or a process remains functional because of its tolerance and resistance to changing conditions; adaptability means that a process or a system can change in response to its conditions in ways that enable it to maintain some state or objective (Gerhard and Kirschner 2007). Instead of falling apart, robustness, adaptability, and integration enable developmental systems to respond to changes in context by adjusting their phenotype, affording them the ability to adjust to stressful conditions (Sultan et al. 2021). For example, *Polypterus* fish reared in a terrestrialized environment lack the ability to swim and are forced to ‘walk’ with their pectoral fins; within a lifetime, their behavior, gait, posture, and skeletal features adjusted to accommodate their environmental conditions in ways that mirror anatomical changes in ancient tetrapods’ moving from water to land (Standen et al. 2014, cited in Sultan et al. 2021). Numerous other examples demonstrate that the interaction between developmental systems and the environment, especially in the face of novel or stressful conditions, may result in the production of useful, integrative, and potentially adaptive phenotypic variants (Sultan et al. 2021). This does not suggest that genes are not important players in the origin of evolutionary novelty, as genes are essential in enabling modularity and responsiveness in the first place. Rather, phenotypic variation is also generated thanks to the responsiveness and creativity of developmental systems and therefore should be considered, in addition to the role of mutation, when attempting to understand the nuances of evolutionary innovation.

Conclusion

Biological agency is an exciting approach because it offers a system-to-component direction of explanation that highlights the agential dynamics of living systems and is capable of accounting for the ways in which the activities of the system as a whole are both context-sensitive and capable of regulating its activities, structures, and relations in pursuit of goals, or stable endstates (Sultan et al. 2021). Organisms' systematic modulating their parts and processes in context-specific ways is a unique feature of agential systems that cannot be accounted for using a context-insensitive genetic determinist approach, but is illuminated through the complementary biological agency perspective. Moreover, the biological agency perspective is crucial both pragmatically and methodologically, as well as philosophically, because it helps overcome the explanatory gaps left by prevailing gene-focused approaches. It is important to recognize that one of the primary reasons biological agency is able to provide this enhanced account of organismal life that is missing from a gene-centric approach is because it recognizes organisms not as mechanical objects, but as living agents with properties distinctly unlike nonliving entities. Agents are responsive instead of reactive, context-sensitive instead of context-insensitive, purposive instead of deterministic...

One of my key takeaways from the biological agency approach was its implicit emphasis on relationality—relationality between component systems within the organism to other systems, to the organism itself, and to the organism's environment, relationality between the organism's genetics as mediated by its engagement with its environment, and the list goes on. Through its emphasis on the dynamic, responsive, and context-sensitive nature of agential systems, the biological agency perspective suggests that these overlapping and interwoven relationships are organic, rather than mechanistic; they seem to be formed out of a process or interaction that

emerges and plays out in a specific context, and therefore cannot be known entirely in advance or abstracted from their unique context as might be the case for a nonliving entity whose properties are insensitive. While this emphasis on relationality is one of the features of a biological agency approach that enables it to serve as a productive complement to component-to-system approaches, biological agency's account of relationality could be strengthened. For example, a biological agency approach illuminates the networks of interactive relationships at play in organismal systems and sets them apart from machines. However, a biological agency approach's account of relationality does not extend beyond the organism—it does not include the scientist, research relationships between scientists and organisms, or how the scientist's relationality may inform their research relationship with organisms. Many voices speaking from feminist epistemology and feminist science studies explore the role of subjectivity, embodiment, and relationality between subjects. In Section 4, I will introduce some of the voices speaking from these perspectives and explain how they build off and broaden biological agency's emphasis on relationality by questioning further into the relationship between the organism and the scientist, as well as the scientist's particular relational embeddedness.

Section 4

By illuminating organisms' agential dynamics—their ability to respond adaptively to their conditions—the biological agency perspective crucially points out that organisms, in being agents, are distinctly unlike machines and therefore cannot be studied solely from a genetic deterministic perspective. The dynamics of machines can be “exhaustively explained by appeal to the structure and activities of its parts” and completely captured by the component-to-system direction of explanation (Sultan et al. 2021). However, organisms require a system-to-component direction of explanation because the structure and functioning of component parts of agential systems are regulated in part by the activities of the agent as a system and through its engagement with and responsiveness to its environment (Sultan et al. 2021). Genetic deterministic approaches center and prioritize an organism's genes, isolate component parts, and attempt to discern linear causality in order to understand processes like evolution, development, and inheritance. Conversely, the biological agency approach reveals that genes, biology, organisms, and environments are so interconnected and mutually entangled that attempting to study organisms by isolating their genes results in explanatory gaps. Accordingly, the biological agency perspective reveals the importance of understanding living things not as context-insensitive, genetically determined, or decomposable entities, but as sensitive and responsive beings embedded in and made up of a multitude of co-constitutive relationships. This perspective suggests the need for a shift in the biological sciences away from a completely gene-centric framework and mechanistic view of life and towards a more relational one that can account for the ways in which organisms are uniquely unlike machines.

Compared to gene-centric approaches, biological agency is certainly a step toward a more relationally oriented scientific framework and understanding of life that bring with it new

responsibilities and implications for biological inquiry. By revealing the organism's relationship to its environment, for example, the biological agency approach simultaneously conveys that scientists studying organismal processes in terms of genes are obliged to consider the ways in which the genes may be sensitive to certain environmental variables. However, as I engaged with the biological agency perspective more deeply and came to understand how its framework is grounded in an emphasis on relationally-contingent sensitivity and responsiveness as opposed to isolation and determinism, I began to see more degrees of relationships—that similarly come with new sets of responsibilities and implications—that the biological agency approach was not accounting for but seemed crucial to a non-mechanistic understanding of life.

My engagement with the biological agency perspective happened alongside engagement with scholarship from feminist epistemology and feminist science studies, which similarly emphasize relationality in their discussion of and approach to scientific inquiry, but question further in their accounts of relationality to include the scientist's relational embeddedness and the many intersecting and co-constitutive relations as they come to inform research relationships and scientific inquiry. These feminist approaches implicitly build from biological agency's account of relationality by extending it to include the scientists themselves in order to demonstrate that they too are relationally situated and co-constituted. Recognizing that scientific inquiry itself is a relational, subjective, situated, and embodied practice reveals numerous practical implications and new responsibilities that may strengthen biological agency by deepening its account of relationality through demonstrating that biological scientific inquiry is relationally dependent and embodied and needs to be recognized as such.

In this section, I draw from perspectives in feminist epistemology and feminist science studies in order to offer an account of relationality and its features that deepens biological

agency's perspective on relationality. I explain the feminist framework's centering of the body and how it invites us to see that science is already an embodied practice and that our theorizing is situated and subject-related. Realizing that our science is a subject-related, embodied, relational practice by no means compromises objectivity or the quality of science we are able to do; instead, committing to recognizing our subjectivity and reembodying our practices may deepen the biological agency's perspective of relationality by lowering the boundaries between the scientist and the organism being studied, enabling scientists to develop a more adequate account of objectivity, encouraging an openness and curiosity to relationships, and inviting scientists to recognize how their relational positionality informs their biological inquiry.

In the following sections, I explain each of the following points in depth and how they might strengthen the biological agency perspective as a complementary approach to gene-centric approaches to studying organisms. I intend this discussion to *build* off my discussion of biological agency as a complement to gene-centrism. Instead of using these feminist perspectives to directly respond to gene-centrism's limitations as I did with the biological agency perspective in Section 3, I am interested in putting feminist epistemology and science studies in conversation with biological agency. I am putting these feminist perspectives in conversation with biological agency in order to demonstrate the ways in which they deepen its account of relationality and therefore strengthen it as a complementary approach to gene-centrism by adding the new perspective that biological scientific inquiry is performed by embodied researchers.

4.1 Relationality applies not only to the organism's relationships, but to the scientist's relationships

Through centering the body in its analysis, I will show how a feminist critique may serve to deepen biological agency's account of relationality by dissolving boundaries between the

scientist and other beings and entities and inviting scientists to recognize themselves as members of research relationships, instead of isolated observers. I explore the ways in which centering the body and recognizing it as a culturally coded and relationally formed entity also dismantle the assumption that scientific objectivity is purely impartial and value neutral by showing that scientists are not faceless, universal, or detached observers, but particular, relationally-constituted members of many intersecting relationships. I will then show how recognizing that bodies are not isolated entities but open to and constantly formed and transformed by their experiences (which the scientist is not exempt from) invites us to consistently reflect on and strive to acknowledge how our embodiment and the particular assumptions implicated in our subjectivities are reproduced in our engagement with the world, scientific or otherwise. Much like scientists are constantly being formed and transformed by their relationships, other bodies with which one shares relationships are also consistently being shaped and transformed by their specific context(s). Recognizing the processual and emergent nature of relationships also reiterates biological agency's emphasis on organismal relationality by demonstrating that organisms' context-specific dynamics may not remain constant between individuals, over time, or across different conditions and therefore require a commitment to sensitive, open attentiveness on behalf of the scientist.

I will leverage these insights, among others, to demonstrate that spaces of scientific inquiry are never isolated from our subjectivities and to reveal the importance of softening the boundary between the subject and object of study that inhibits recognizing scientific inquiry as a relational project. Throughout this section, I will explore the ways in which the insights I discuss from the feminist account of relationality, subjectivity, and embodiment serve to deepen biological agency's account of organismal relationality and build appreciation for more holistic

and relational, as opposed to mechanistic and context-insensitive, approaches to studying organisms as agents.

4.1.1 The body and subject

The feminist framework centers the body as its primary site of location (Braidotti 1991). The subject within the feminist framework is not an abstract entity, but rather a “material embodied” entity, allowing for the recognition the body not as a natural thing but instead as a “culturally coded socialized entity” (Braidotti 1991, 160). Recognizing the subject as embodied further serves to demonstrate that the body is “neither an essence nor a biological density, but rather one’s primary location in the world, one’s situation in reality” (Braidotti 1991, 160, paraphrasing Spivak 1987). Dismantling the assumption that bodies are natural things but socialized entities is important because it demonstrates that bodies are not essential, isolated, or determined but rather are constituted in and through their experiences and relationships (Haraway 1998).

The fact that bodies are formed in and through their relationships suggests that bodies are open entities that are affective to their relations, further revealing that any boundaries we attempt to erect within the physical body, between the physical body and our ecologies, or between bodies are “permeable, silted, breathing, and relational” (Voyles 2015, 218, quoted in Kenney 2019, 11). A common boundary in Western scientific tradition that the feminist framework calls into question is the boundary between the subject and object of study that enables the scientist to “transcend the particularities of experience to achieve objective purity and value neutrality” (Code 1996, 194). Through her emphasis on embodiment and subjectivity, feminist epistemologist Lorraine Code refutes Western science’s “professed disinterestedness” and ideals of pure objectivity and value-neutrality that attempt to blur the connection between knowledge

and power by demonstrating that “knowledge is a *construct* produced by cognitive agents within social practices” (Code 1996, 191), “‘facts’ are always infused with values” (Code 1996, 204), “Evidence is selected, not found, and selection procedures are open to scrutiny” (Code 1996, 205). Similarly, taking subjectivity into account is important to recognizing that the boundary of objectivity and value neutrality that claims to isolate the scientist from their relationships—relationships to themselves, to the being(s) they are studying, to the place they are studying, etc.—is only nominal. Just like the body within the feminist framework is not isolated or determined, but situated in and co-constituted by a network of relationships, “knowers are always somewhere—and at once limited and enabled by the specificities of their locations” (Code 1996, 213). Accordingly, a “knower’s subjectivity is implicated, from its earliest developmental stages” and, as such, is produced and reproduced in their work (Code 1996, 212). Since the scientist’s particular positionality informs and is reproduced in their work, locating their inquiry within the context of their relational activity can yield important epistemological insights into their inquiry (Code 1996).

Centering the body and taking subjectivity into account reveals that science is already an embodied practice, but must be recognized as such in order to challenge the mistaken and impossible “ideal objectivity of the universal knower” (Code 1996, 206). Considering the mutually constitutive subjectivities at play in research relationships does not compromise objectivity. Rather, it is the “recognition that rocks and cells, and scientists, are located in multiple relations to one another, all of which are open to analysis and critique” (Code 1996, 210) that calls for a “realistic commitment to achieving empirical adequacy that engages in situated analyses of the subjectivities” of all members of the research relationship that are both particular and mutually informative (Code 1996, 206). Paralleling Code’s critique and Harding’s

notion of “strong objectivity,” Haraway unveils the irony of objectivity within the Western scientific tradition by pointing out that “Objectivity turns out to be about particular and specific embodiment and definitely not about the false vision promising transcendence of all limits and responsibility” (Haraway 1988, 582). Instead of a faceless positionality that ensures scientists do good, unbiased science, this Western notion of objectivity, “that view of infinite vision,” is “an illusion, a god trick” (Haraway 1988, 582).

Haraway posits that a feminist critique of the supposedly disembodied universality and transcendence of Western scientific inquiry calls for a more adequate account of objectivity that accommodates embodied subjectivity. She refers to this account of objectivity as “feminist objectivity” (Haraway 1988, 581). Feminist objectivity simply means *situated knowledges* (Haraway 1988, 581). Haraway’s definition of feminist objectivity as *situated* implies a particularity embedded, or situated, in a fabric of other interwoven particularities; the plural *knowledges* challenges Western epistemological hegemony by advocating instead for knowledges as being one-through-many, accommodating the tension between particularity and collectivity by revealing that the two are not mutually exclusive. Moreover, while the Western account of objectivity promises “transcendence and splitting of subject and object,” feminist objectivity emphasizes “limited location and situated knowledge” (Haraway 1988, 581).

A biological agency perspective demonstrates that it recognizes organisms’ bodies as open and contextually- and relationally-constituted entities through its emphasis on the organism’s context-sensitivity. However, the biological agency perspective’s account of relationality and context sensitivity does not go far enough in understanding relationality because it neither includes the scientist’s context-sensitivity and relationality nor accounts for how their subjectivity and relational-situatedness may be implicated in their account of an organism’s

agential dynamics. Similarly, although a biological agency perspective emphasizes the importance of taking organismal sensitivity and responsiveness into account, it could benefit from inviting the scientist into this discussion by reminding them that the particular context eliciting the organism's context-sensitive dynamics cannot be taken for granted as unchanging, and the organism(s)'s response may not be universal or generalizable. Combining the feminist account of objectivity and analysis of the dynamics of embodiment with a biological agency perspective may deepen its account of relationality in numerous ways. For example, these feminist perspectives encourage the scientist to recognize themselves in the research relationship and challenge the scientist not to assume they know how specific organism(s) will respond in any given context. Through their emphasis on embodiment and situatedness, the feminist perspectives I have explored also reveal that all individuals of a species will respond uniformly to a given condition, that results from one individual are not necessarily translatable to other individuals from different places with different relationships, and that individual(s)' specific context-sensitive response will remain constant even if the condition remains the same.

4.1.2 Embodying and relationalizing science enables response-ability

Through its centering of the body and the subject, the feminist framework reveals that science is already an embodied practice, and the scientists themselves are not transcendent, faceless, universal, or purely objective viewers detached from the object of study because they are implicated in a network of co-constitutive relationships that they reenact in their scientific interactions. Recognizing that science is, in fact, an embodied practice is important to challenging the Western scientific paradigm that justifies systems of domination, bias, exclusion, discrimination under the guise of ideals like pure or detached (impartial) objectivity and neutrality, and opens the possibility for redefining the systems, beliefs, and practices that

perpetuate detached, disembodied science. Recognizing that biological scientific research is a subjectively dependent practice performed by embodied researchers is vital because it helps build appreciation for holistic and relational, instead of mechanistic and particulate, approaches to studying organismal agency. Building recognition and appreciation for holistic and relational approaches to studying organisms also creates space for seeing how these approaches are not just conceptual frameworks but actionable methodologies that can be implemented onto practical biological agency approaches to studying organisms.

Recognizing that Western science is an inherently embodied practice informed by our situatedness and subjectivity enables what feminist science scholars such as Martha Kinney, among others, have termed *response-ability*. Response-ability is a feminist ethic that advocates for cultivating and creating space for different kinds of responses in our interactions (Kenney 2019, Schrader 2019). Response-ability is a “term that might whet our imaginations for more relational ethics and politics enacted in everyday practices of living in our more-than-human world” (Kenney 2019, 7). Response-ability emphasizes openness to relationships, mutual affectivity, and curiosity in the sense that one does not go into an interaction with preformulated assumptions, but rather with an intentional openness to learn out of and from the interaction; Kenney writes, “What counts as response-ability is not known in advance; it emerges within a particular context and among sometimes unlikely partners, who learn how to affect and become affected by one another” (Kenney 2019, 7). Much as bodies are not stagnant, essential, isolated, or determined entities but are constantly being co-constituted by and through relationships, the feminist ethic of response-ability reveals the organic processuality of relationships by demonstrating that learning how to affect and become affected in relationships is a constant,

interactive process that is not known in advance but emerges out of the relationship and as it is maintained.

Code reiterates the organic, processual nature of relationality that requires a commitment to constantly learning when she claims that the fluctuations and contradictions of subjectivity—the fact that subjectivity is never fixed or complete—means that getting to know the self and its relationship to other selves is an ongoing, communicative, interpretive process (Code 1996). She writes, “Knowing other people in relationships requires constant learning: how to be with them, respond to them, act toward them. In this respect it contrasts markedly with the immediacy of common, sense-perceptual paradigms” (Code 1996, 209). Code’s statement about knowing others in relationships does not only apply to relationships between humans, but can also be used as a framework for learning about other organisms, both inside and outside of research relationships. This framework, as Code articulates it, promotes the idea of relationality as responsibility to other member(s) of the relationship, instead of relationality with the intention of meeting baseline research ethics guidelines.

Recognizing that scientific inquiry is an embodied and relational pursuit reveals another dimension of Haraway’s *situated objectivity* and Harding’s *strong objectivity*: if we are always situated in, being formed by, and forming relationships, then we are responsible for continually learning about these relationships as they evolve and recognizing how they inform our scientific inquiry. Code’s emphasis on relationality encourages scientists to consider themselves as a *member* of a particular research relationship, instead of an impartial, universal, or detached observer. Moreover, Code’s statement that knowing other people in relationships requires constant learning also reiterates the processuality of relationships in the feminist ethic of response-ability, but reveals a paradox: *learning* about someone is an ongoing process, but

knowing someone, as I have been taught in a traditional Western classroom and society, implies that I can trust someone to remain constant and fixed within the bounds I have learned to be true. Accordingly, I believe Code's point about how the ongoing-ness of subjectivity necessitates constant learning to know someone as it relates to the ethic of response-ability is actually suggesting that *knowing* others is not attainable; rather, we should strive to be constantly learning about others with open, curious attentiveness.²³

The ethic of response-ability as it follows from the feminist centering of the body and subjectivity offers a "vision of biology as the pursuit of passionate, embodied inquiry" and shows that "there are other ways of knowing than the disembodied and disinterested version of scientific objectivity that we see in more official histories of evolutionary biology" (Kenney 2019, 14-15). Accordingly, response-ability offers scientific inquiry through the biological agency approach an opportunity to recognize that working with organisms is an embodied,

²³ I want to clarify that curiosity and openness to learning do not imply or promise that one will always be able to learn and eventually understand other beings, nor should this be the ideal one strives for in their interactions. Learning about someone is not synonymous with understanding them or being able to personally relate to them; similarly, learning about someone cannot be done in isolation from learning about oneself and that which one does not understand, relate to, or share in common. When I refer to an openness and curiosity to learning, I am attempting to invoke the ongoing-ness of learning, and the importance of holding space for process and unpredictable but possible possibilities for growth, interaction, and future learnings about oneself, others, and one's relation(s) to other(s). Additionally, openness and curiosity as I intend them also refer to one's relationship with learning about oneself and one's relationship to others, and not just to learning about others. By this, I mean that openness and curiosity require introspective inquiring into that which one may never be able to learn about and/or will never be able to learn about. Although there may be instances where learning about others may be something that comes with discovering a shared experience, solidarity, or finding mutual understanding, this is not something one can or should expect from all encounters and learning processes. Similarly, one should not expect or be entitled to learning interactions, especially as it refers to interactions with others from underrepresented or marginalized identities and groups. Accordingly, I intend openness and curiosity to refer to a commitment to learning about oneself, and recognizing and holding tension for learning as learning and not learning as understanding or knowing.

intersubjective encounter and therefore requires a curious openness to learning through the encounter and a commitment to cultivating and maintaining response capacity. While establishing certain parameters in experimental designs necessitates entering into scientific encounters with some extent of pre-interaction expectations, response-ability encourages scientists to create space for unexpected responses and learnings that might emerge through the encounter. Cultivating this response capacity and prioritizing curiosity and openness to the fact that the organism is also a subjective entity with the capacity to both call, respond, and transform through the interaction mitigates the likelihood that pre-interaction expectations erect subjective biases that keep the scientist from learning through and from the interaction itself or create subconscious or conscious blinders that blur or restrict the scientist's fine-tuned and inclusive attentiveness. Response-ability, in positing that knowing an other is never complete, could benefit a biological agency approach because it encourages scientists to refrain from assuming that they know how an organism will respond and instead keep interactions open, which may increase attentiveness to the nuances of context-sensitive dynamics and encouraging scientists to commit to continuously learning through the interaction, instead of artificially constraining the timeline under which the interaction is allowed to take place.

Conclusion

The biological agency approach offers many implicit critiques of mechanism and genetic determinism. For example, while a purely deterministic and mechanistic account of organisms assumes that organisms are closed, context-insensitive entities by proceeding to study them through their genetic constituents, the biological agency approach reveals the sensitive, responsive nature of organismal life by dissolving the genetic deterministic barrier separating the organism and its genes from the environment.

As I have shown, the biological agency approach makes it clear that organisms are embedded in and made up of entangled networks of consistently changing relationships and processes, whether they be genetic, intra- or intercellular, or otherwise intraorganismal, or environmental, which calls into question the viability and relevance of creating mechanistic boundaries to separate and causally discern organismal processes in the first place. While the biological agency approach is important progress in the Western scientific tradition as an approach that emphasizes the relationships inside organismal systems and their connectedness and sensitivity—as opposed to separation from and insensitivity to—their environment, feminist science studies and epistemologies center the body and the subject in order to advocate for a deeper form of relationality that also includes the scientist themselves, and invites them to commit to certain intersubjective responsibilities that add another level of nuance to the biological agency’s account of relationality.

Opening the boundaries between, within, and beyond subject and object that perpetuate a misguided sense of objectivity, disembody and disaffect research, stifle intersubjective relationality and mutual affectivity, and contribute to the scientist’s positionality as an isolated, transcendent, universal observer is essential to deepening and expanding biological agency’s account of relationality. Through an emphasis on the body, embodiment, and subjectivity, I have explored some of the ways that feminist thinkers question further into biological agency’s account of relationality by opening the subject-object boundary, among other relationally-stifling boundaries. They also recognize that the embodied nature of science calls for a deeper understanding of relationality that includes the scientist and their relationships, necessitates the redefinition of objectivity, and reveals the ethic of response-ability.

Recognizing that biological scientific research is a subjectively dependent practice performed by embodied researchers builds off biological agency as a complement to gene-centrism and cultivates appreciation for holistic and relational—instead of context-insensitive, detached deterministic, or purely mechanistic—approaches to both studying organisms and conducting oneself in research relationships.

Conclusion

This thesis began as an exploration of the limitations of gene-centric approaches to studying organisms, but, after many months of grappling with this question, following it into rabbit holes, spending countless early mornings and late nights researching it, I watched as my original question evolved and grew to accommodate everything I learned along the way. I can't say I ended up where I thought I would, but this has been part of the fun—and frustration—of it all.

I started this thesis by exploring what might be missing from gene-centric, deterministic and mechanistic accounts and methods of studying organismal life, and how these potential limitations might be manifesting paradigmatically and practically, in how we learn about and are influenced by science and how we do science. Exploring the limitations of gene-centric and mechanistic accounts of organismal life brought me to alternative approaches, and eventually the biological agency perspective. Through emphasizing the features of organisms that set them apart from machines, the biological agency perspective seemed able to not only illuminate the explanatory limitations of gene-centric approaches to studying organisms, but offer complementary ways of studying organisms that could overcome the limitations associated with a gene-centric method. Intrigued, I continued writing my thesis with the intention of learning about and exploring the idea of biological agency as a means to challenge genetic reductionist approaches to studying organisms.

At the beginning of this process, biological agency was an incredibly abstract metaphor for a non-mechanistic approach to studying life that I struggled to articulate let alone understand—it offered a framework and suggestions for incorporating an agency perspective into research programs that challenged my conception of research designs, as well as a vocabulary for

talking about and studying organisms that was completely new to me. I was not familiar with talking about organisms as responsive and environmentally-sensitive agents or conceiving of their activities and processes as purposive, and I had only recently began learning about context-sensitive dynamics like epigenetic inheritance. I was especially fascinated with the way that the agency perspective helped reveal explanatory gaps left by gene-centric approaches to studying organisms, which left me questioning, “What about prevailing gene-centric approaches is leading to these limitations in the first place?” While the biological agency perspective helped identify these gaps, there was minimal discussion of the scientific assumptions or systematic factors leading to these gaps in the first place and further necessitated a complementary biological agency approach.

I did not expect to find myself questioning why the limitations of gene-centrism were happening in the first place—this questioning initially seemed to be steering me off track from my original intention of exploring biological agency as a means to question genetic reductionism, but I later came to realize it was an incredibly important part of the story. By delving into the history of the gene-centric approach to studying organisms, I began to see that its limitations are connected to and may be stemming from the story we have been taught to believe about organisms and how we should be studying them in Western science. Perspectives like Dawkins’, for example, are indicative of a lineage of mechanist and reductionist paradigms and methodology in the Western scientific tradition that obscure the organism itself—its spontaneous engagement with the environment, its activities that indicate reciprocal interactions between development and environment...— and reduce it to the passive object of its genes’ predeterminations. This brought me to see how the unique features of biological agency that gene-centrism is lacking is an attention to the organism itself as not only agential, but

*relational*²⁴—agential dynamics like context-sensitivity and reciprocity between development and environment would not be possible if the organism was merely a passive object isolated from its environment. Agential dynamics rely on there being relationality between component systems within the organism to other systems, to the organism itself, and to the organism's environment, relationality between the organism's genetics as mediated by its engagement with its environment, and the list goes on. Through its emphasis on the dynamic, responsive, and context-sensitive nature of agential systems, the biological agency perspective suggests that these overlapping and interwoven relationships are organic, rather than mechanistic; they seem to be formed out of a process or interaction that emerges and plays out in a specific context, in a unique merging of relationships, and therefore cannot be known entirely in advance (i.e. determined solely by the information encoded in genes) or abstracted from their co-constitutive context as might be the case for a nonliving entity like a machine whose properties are context-insensitive. This is why biology needs a biological agency perspective.

The attention to organisms' relationality and context-dependence is integral to the biological agency perspective and distinguishes it from the complementary system-to-component, gene-centric approach to studying organisms. However, upon closer analysis and exploration of scholarship from feminist epistemology and feminist science studies, I began to see that biological agency's account of organismal relationality, while certainly novel as a complement to gene-centrism, was still limited. For example, although the biological agency

²⁴ Whether this be the relationships within a cell, between cells, between the organism and certain genes, between organisms and their environment, or other relationships. Instead of being completely determined by their genes or passively shaped by their environment, the biological agency approach draws on the idea of the organism existing within a network of interconnected and co-constitutive relations to which the organism is sensitive and response to in order to demonstrate that the organism must be understood in the context of these relationships, as opposed to solely through their genes.

perspective implicitly revealed that some of the limitations of gene-centric approaches can be tied back to its inability to recognize the interconnected and disentangle-able relationships between the environment, organisms, biology, and genes, the biological agency perspective does not consider relationality beyond the organism itself as the object of study in scientific inquiry. Certainly, the organism itself, and its activities and engagement with the world, is relevant to consider so as to overcome the limitations of gene-centrism and more accurately represent organismal dynamics, but what if there were more relationships beyond just the organism itself that are relevant to consider for not only overcoming gene-centrism's limitations, but understanding why they might be happening in the first place and using this as a lens through which to begin eradicating these structural barriers? Through inquiring into the history of Western scientific inquiry through the frameworks afforded by scholarship from feminist epistemology, feminist science studies, and decolonial science, I began to see that relationality extends beyond the organism as the object of study to include the relationship between the observer and the observed, the observer's relationships, and so on.

Deepening and expanding biological agency's perspective of relationality—which brings with it an emphasis on embeddedness, embodiment, situatedness, and subjectivity—illuminates new layers of relationships beyond those discussed in biological agency, each of which come with new sets of responsibilities and commitments, that can, in turn, serve as opportunities for how we may do better science. I was (and am) both inspired and challenged by the implications of the perspective of relationality I learned from feminist epistemologists, and scholars in feminist science studies. When the knower, the scientist, is recognized not only as an intimate member of the research relationship, but also as a relationally constituted and relationally embedded being, the distinction between research and everyday life, between “being and doing”

becomes incredibly blurry: where does science end and life begin (Liboiron 2021, 133)? The answer seems to be that being and doing, *being* in the world and *doing* science, are not isolated, but always overlapping—I do not stop ‘being a scientist’ when I leave the lab, and my being-in-the world does not stop when I am doing science. Simply, everyday life is science, and science is everyday life. Going forward, I am again inspired and challenged, excited and daunted, by the implications of this conclusion. For me, this exploration has helped reveal what is just the beginning of a network of relationships that I am reconciling, establishing my orientation to, and understanding my role in, if any. My thesis might be over now, but the experiment is never complete; these relationships I’ve met along the way and my connection to them will continue to grow, expand, change.

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