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Glückliche Fügung: Experiments' Potential to Integrate Disciplines**

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Summary: This essay reviews the discipline-connecting potential of experimentation. Two examples are used to illustrate how researchers in the first half of the twentieth century profitably combined resources from different disciplines in their experiments. These experiments were designed to test mechanism models describing chemical processes underlying the behavior of biological systems. The researchers had clear expectations about how certain interventions should affect the behavior of the organisms studied, if that behavior was indeed based on the presumed chemical processes. They manipulated the organisms in the relevant ways and determined how the behavior of the organisms changed as a result.

Keywords: experiment, interdisciplinarity, mechanism model, research organism, manipulation, historiography and philosophy

1. Success through Joining vs. Cracking Joints

Today, as in the past, researchers and science managers have high hopes for the combination of different disciplinary approaches and findings. Botanist Julius Wiesner, for example, urged the search for connections between disciplines, convinced that "the contact of one science with the other sciences yields the richest harvest for all the touching or interpenetrating parts."[1] However,

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[1] Wiesner 1905, on 126. Translation is mine.

coordinating the approaches and concerns of different disciplines is not a trivial matter. Tension may arise because different disciplinary cultures are interested in different aspects of a problem or prefer different ways of solving them. Or because the phenomena under consideration are conceived quite differently, as one biologist noted in 1932:

> Most of the time, physicists have a conception of the *peculiarity* of biological objects and processes which is downright irritating to the biologist, and which consists either in an extremely schematizing and simplifying tendency, or which is content with principles of such general formulation and validity that nothing is gained thereby for the study of a *case at hand*.[2]

Given these difficulties, it is all the more interesting to examine cases in which disciplines were successfully integrated. Here I present two of them and argue that in each case the integration occurred in the context of experimentation—i. e., the purposeful manipulation of a biological system and detection of how the manipulation affects the behavior of the system. The data thus obtained helped the researchers to assess the plausibility of their hypotheses about the chemical processes underlying the behavior of biological systems.

From the examples we can trace how the cross-disciplinary connections became more and more solidified over time. Initially there was speculation about the existence of such connections (section 2). To test these assumptions empirically, the researchers needed *material* interlocking models in addition to the mental ones already present (section 3). In the cases discussed here, these material models were experimental organisms that exhibited the biological behavior under study. The mental models described the chemical processes they believed to underlie this behavior. They informed the way the researchers manipulated their experimental organisms; and how they interpreted the effects of the interventions on the organisms' behavior (sections 4 and 5). In both cases, the disciplines were integrated during experimentation: In planning, executing, and interpreting their experiments, the researchers mobilized resources from the different disciplines and were thus able to solve disciplinary problems satisfactorily (section 6).

The historiographical analysis outlined here focuses on researchers (and their goals, norms, conceptual as well as material resources, and skills) and thus deviates from a historical epistemology à la Rheinberger that understands the history of the life sciences in terms of structures, series, and transformations. This complementary approach lends itself to illuminating the social dimensions of research practice, such as researchers' decisions to collaborate with experts from other disciplines. It moreover invites the application of concepts developed in the philosophy and sociology of science concerning the goals, norms, and organization of scientific practice. And finally, it helps us better understand why researchers make an effort to put fragments obtained in

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[2] Gicklhorn 1932, on 383. Original emphasis. Translation is mine. It is tempting to point out that if biology were replaced by history and physics by philosophy, many historians of science would probably agree with the message. They are puzzled by the schematizing way philosophers deal with historical actors and developments. And they are uncertain whether their analysis of individual cases benefits from consideration of philosophical concepts.

different disciplines into a coherent context in the first place, and how they go about doing so (section 7).[3]

2. Presumed Disciplinary Links (in Purple)

Scientists regularly presume points of contact between fields of research before they can specify them precisely. Take photochemistry and visual physiology as an example. In 1912, physiologist Johannes von Kries (1853–1928) stated that a relation between these two areas undoubtedly existed but was not as close nor as extensive as one might wish.[4] The notion that light might chemically affect the visual cells of humans and animals was indeed not new. It had been around since light's chemical action became known in the 1840s and was further supported by the discovery of a purple substance in the retina of various vertebrates that bleaches out when the animals are exposed to light. Still unknown, however, was the way in which the chemical transformation of this substance caused by light triggers the physiological processes in the narrower sense of the word.[5] Von Kries hoped that research in photochemistry would help to elucidate the physiological process of light reception. Indeed, only a few years later new findings from this field guided the research activities of the young zoologist Selig Hecht (1892–1947).

The fields of organic chemistry and genetics offer a similar example. It was generally assumed that Mendelian factors act chemically and in some way or another govern biochemical processes. However, the specific biochemical effects of individual genetic factors were still in the dark in the 1920s. Contemporary genetics, according to Thomas H. Morgan (1866–1945), blanked out the physiological/biochemical processes influenced by genes.[6] One researcher with expertise in genetics as well as biochemistry, however, had long had a hunch about how the influence of individual genetic factors on biochemical processes could be elucidated: Muriel Wheldale Onslow (1880–1932), née Wheldale, envisioned a chemical-genetic study of anthocyanins, the plant pigments responsible for the red, purple, or blue coloration of flowers and fruits. She believed that uncovering the chemical processes underlying the formation of these substances in the plant cell would also shed light on the action of Mendelian factors and vice versa.[7]

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[3] According to Rheinberger 2021, on 251, historical scholarship and scientific research share the effort to put fragments into context.

[4] von Kries 1912, on 465.

[5] Ibid., on 469.

[6] Morgan 1926, on 489.

[7] Wheldale 1916 and Wheldale Onslow 1925. For more details on Wheldale Onslow, see Richmond 2007.

3. Manipulating Material Models to Consolidate Mental Ones

As we have seen, assumptions have been circulating for some time about how processes studied in different disciplines might be related: animals' perception of light might involve a photochemical process; and the development of colored plant tissue might be caused by genetic factors that control pigment synthesis. We can take these assumptions as sketchy mechanism models, as abstract accounts of the physicochemical processes responsible for the organisms' behavior. Philosophers of science have argued that the practice of setting up and testing mechanism models usually requires the expertise of multiple fields and therefore attributed an integrating effect to the search for mechanisms.[8] Analyzing historical actors' mechanism models is worthwhile not only from a conceptual point of view, but also from a social one: shared mental models help researchers with different disciplinary backgrounds to integrate their knowledge and expertise.[9]

However, cross-disciplinary research requires more than conceptual models. As Margaret Morrison and Mary Morgan argue, "we learn more from building the model *and from manipulating it.*"[10] Hecht's and Wheldale Onslow's work was indeed not limited to hypothesizing about the chemical processes that might occur in the cells of living organisms. Rather, they established experimental systems that were suitable for testing their model assumptions. This test consisted in manipulating living organisms and assessing whether the interventions changed the behavior of the organisms as expected.

4. The Duration of Chemical Reactions in Vitro and in Vivo

A central component of this system was the organism to be manipulated. Hecht made an unconventional but well-considered choice in this respect: He worked with eyeless marine invertebrates such as *Ciona intestinalis* and *Mya arenaria.* Based on the characteristic response to sudden light impulses, the retraction of their siphons, biologists determined that these animals perceived light. Key to the success of Hecht's project was the fact that the velocity of this response varied with the amount of light energy applied to the animals: the higher the light intensity or the longer the exposure time, the faster their response. Hecht moreover found that a constant amount of light energy was necessary to trigger the reaction. The light behavior of the experimental animal thus obeyed the rule that Bunsen and Roscoe had established for photochemical processes. This was a first indication that the immediate effect of light on

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[8] Craver and Darden 2013, on 162–163: "The integration of biology is forged by building mechanism schemas that span many different levels, bridge across many different time scales, and that satisfy evidential constraints from many areas of biology (chemistry and physics too)."

[9] Andersen and Wagenknecht 2013, on 1888.

[10] Morrison and Morgan 1999, on 12. Emphasis is mine.

the sensory cell might indeed consist in the decomposition of a light-sensitive substance.[11]

Mya and *Ciona* were particularly manageable experimentally because their light-response was unambiguous and consistent, but also slow enough that it could be measured with a stopwatch. They also felt comfortable in water of different temperatures. This allowed Hecht to check whether the chemical reaction underlying the sensitization phase was thermostable—as photochemical reactions were known to be. Finally, Hecht had reason to believe that he was dealing with a comparatively simple system.[12]

The ways in which Hecht manipulated his biological models were informed by knowledge established in physical chemistry. With light intensity and wavelength, exposure time, and temperature, he varied factors whose influence on the course of chemical reactions had already been determined in vitro. Publications like Fritz Weigert's 1911 book *Die chemischen Wirkungen des Lichts* provided him with expectations about how the manipulations should affect the duration of the animals' reaction, if this reaction really was based, as hypothesized, on a photochemical reaction followed by a normal chemical reaction.

5. Isolates from Known Genotypes and Syntheses of Known Structure

Wheldale Onslow also had a clear idea of which plants were suitable for her study: varieties of *Lathyrus odoratus* and *Antirrhinum majus* in which crosses between individuals with white and ivory flowers (neither of them contain anthocyanins) give rise to individuals with magenta (i. e., anthocyanin-containing) flowers. She explained that "In these well-known varieties lies the secret, as yet unrevealed, of the biochemical reactions which control the formation of anthocyanin."[13] According to Wheldale Onslow, organic chemistry provided the methods for the isolation and structural analysis of anthocyanins while Mendelian methods allowed to determine the laws of their inheritance. "By a combination of these two methods," she argued, "we are within reasonable distance of being able to express some of the phenomena of inheritance in terms of chemical composition and structure."[14] For the period between 1907 and 1915, when she herself was working on the project, this diagnosis was too optimistic. But in 1929, Wheldale Onslow urged her graduate student Rose Scott-Moncrieff (1903–1981) to resume the project, because the organic chemist Robert Robinson (1886–1957) had since succeeded in synthesizing a number of anthocyanins. Scott-Moncrieff, for her part,

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[11] Hecht 1918b.

[12] Hecht knew little about the structure of the sensory cells of his experimental animals but assumed that they possessed only one type of visual sensory cells (unlike, for example, frogs or humans with their rods and cones).

[13] Wheldale Onslow 1931, on 373.

[14] Wheldale 1916, on vi.

was skilled in isolating natural anthocyanins from plants. Furthermore, Wheldale Onslow's colleague J. B. S. Haldane (1892–1947) had recently became head of research at the John Innes Horticultural Institution (JIHI), which had plants with well-established genotypes.[15] In the summer of 1929, Scott-Moncrieff started to cooperate with both disciplinary groups. "The idea," she later recalled, "was to correlate the synthetic breakthrough with isolations + identifications of the natural pigments + the genetic relationships which were emerging from the J. I. material."[16]

The project soon bore its first fruits. Scott-Moncrieff was able show that single genes are responsible for simple biochemical differences. Her first finding was based on the inheritance pattern of the pink *Pelargonium zonale* variety Constance. A self-cross resulted in seventeen offspring with pink and three with salmon flowers, the "latter colour being clearly recessive." Scott-Moncrieff isolated the pigments and identified in the pink flowers "cyanin, a slight trace of pelargonin, and an appreciable amount of flavone," while the salmon flowers "contained only pelargonin with a trace of flavone."[17] According to Robinson and his collaborators, the only structural difference between the two anthocyanins cyanin and pelargonin was that the former possessed an additional hydroxyl group at position 3′. From these genetic and chemical clues, Scott-Moncrieff concluded that the "effect of the factor which converts salmon into pink is, therefore, to substitute cyanin completely for pelargonin, the difference being that of a single oxygen atom."[18] Haldane noted enthusiastically, "This is the first case in which a factor has been shown to convert a definitely characterized substance A into another substance B."[19]

6. Experimentation as Integrating Practice

In both cases, the different disciplines were integrated in the course of experimentation. Hecht used findings from physical chemistry to characterize the chemical system underlying *Ciona*'s and *Mya*'s light response. He later explained that the photochemical literature provided "knowledge which could be drawn on for an understanding of the nature of vision and photoreception."[20] The concepts of physical chemistry attributed meaning to his

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[15] On Haldane's John Innes years, see Wilmot 2017.

[16] Rose Meares (née Scott-Moncrieff) to Richard Synge, 25 May 1975, Papers of Richard Synge, Trinity College Library, Cambridge, UK, J. 195.

[17] Scott-Moncrieff 1931, on 974.

[18] Ibid., on 974–975.

[19] John B. S. Haldane, JIHI-internal Report for the year 1930, on 5, John Innes Archives, Norwich. A few years later, Scott-Moncrieff revised her original analysis. The second pigment in *Pelargonium* turned out to be malvidin 3–5dimonoside instead of cyanine. In Scott-Moncrieff 1936, on 150, she emphasized that her original argument was not affected by the revision: "a genetical factor is here responsible for a flower-colour change involving a more oxidised superficial structure of the anthocyanin aglycone, while leaving the glucosidal residue unchanged."

[20] Hecht 1938, on 22.

manipulations and their effects on the behavior of the experimental animals. Scott-Moncrieff, in turn, used genetic interventions (crossing of postulated genotypes) and chemical methods to identify the pigments produced in vivo.[21] This allowed her to relate specific biochemical changes to single genes and to corroborate or reject assumptions about anthocyanin biosynthesis. Unlike Hecht, she did not have to build a new experimental system from scratch, but rather linked to their mutual benefit two experimental systems running in parallel.

Both cases underscore the material condition of the research activity that philosophers characterize as the search for mechanisms. For such a cross-disciplinary endeavor to work, the fields in question must be brought together not only conceptually, but also experimentally.[22] Researchers need a suitable biological system to test their mechanism models. The fruitful study of the chemical basis of light perception and color expression hinged on the discovery of biological systems that (a) exhibit the behavior under investigation (i. e., perceive light or produce red, purple, or blue flowers), (b) can be manipulated in the relevant ways (variation of stimulus and stimulated system; re-arrangement of genes by crossing), and (c) in which the effect of the manipulations can be traced (velocity of animal's light-reaction; structure of the pigments produced).

Through the activity of experimentation, Scott-Moncrieff and Hecht accessed hidden subcellular processes. Now, experimentation does not proceed in a random manner, but along investigative pathways. Researchers' knowledge and skills determine which research problems they decide to work on.[23] Knowing their personal pathways—where and how they were trained and what they aspired to—helps to better understand their research actions. Wheldale Onslow's project plans were clearly informed by her previous studies on the inheritance of flower color in species such as *Antirrhinum majus.*[24] Similarly, Hecht was already familiar with the anatomy and physiology of ascidians before he decided to use *Ciona intestinalis* to study the mechanism of light reception.[25] Biologists' experience in dealing with organisms and their familiarity with the organisms' behavior therefore seems to be crucial in identifying starting points for biophysical or biochemical experiments.[26] On the other hand, Wheldale Onslow's and Hecht's proceeding would be hardly compre-

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[21] By demonstrating that the pigments she isolated from plants grown at the JIHI had the same properties as the syntheses produced in Robinson's laboratory, Scott-Moncrieff established the identity of the substances and the link between the two fields.

[22] See Rheinberger 2000 for a detailed account of how Alfred Kühn and his coworkers established and developed an experimental system that combined genetics, development, and physiological chemistry into a unified approach.

[23] Nickelsen 2022, on 33.

[24] Wheldale 1907.

[25] Hecht 1918a.

[26] For another example on this point, see Kathryn Maxson Jones' contribution in this issue.

hensible without the insight that they wanted to uncover subcellular mechanisms according to contemporary disciplinary norms.[27]

7. *Glückliche Fügungen* and Exciting Gaps

According to Scott-Moncrieff, knowledge of the genetical factors controlling color variation in plants was "furthered by fortuitous coincidence of chemical and genetical study by independent workers."[28] By integrating two lines of work, Scott-Moncrieff and her collaborators gained spectacular new insights into the biosynthesis of anthocyanins, i. e., the action of genes. Hecht argued in more general terms that "a sudden forward movement in one science has often consisted in the application of a principle from a distantly related field."[29] In fact, by applying principles from physical chemistry, he was able to elucidate the mechanism of light reception according to the methodological norms of sensory physiology.

But what about the concerns of the biologist quoted at the beginning of this article about the inappropriate simplification of biological processes by physicists? Notably, Hecht readily admitted that "the photoreceptor process itself is certainly more elaborate" than his model depicts and that "vision involves more than the photoreceptor process alone." Yet he found it very interesting "that the behavior of many visual functions may be formulated in quantitative detail in terms of these minimum essentials alone."[30] Looking at our historiographic analysis, it is equally remarkable how many aspects of Hecht's and Scott-Moncrieff's research activities can be explained by reference to their goal of studying the mechanism of light perception and anthocyanin formation alone—from the selection of experimental organisms, to the way they manipulated them and interpreted the effects of the manipulation, to the collaborations they entered into. The general assessment that they succeeded in achieving this goal, moreover, explains the enthusiastic reception of their

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[27] Hecht 1925, on 66, emphasized that his study met the criteria of Beer, Bethe, and von Uexküll 1899 for the objective study of sensory physiological processes. Wheldale 1916, on v, reminded her fellow geneticists that a "proper conception of the inter-relationships and inheritance of the manifold characters of animals and plants will be greatly facilitated by a knowledge of the chemical substances and reactions of which these characters are largely the outward expression."

[28] Scott-Moncrieff 1936, on 118.

[29] Hecht 1922, on 6.

[30] Hecht 1938, on 39.

work.[31] Anthocyanins and visual purple, finally, remained popular objects of study for scientists interested in integrating chemistry and biology.[32]

Experiments have the potential to integrate disciplines; not only the physical and biological sciences, but also the historiography, philosophy, and sociology of the life sciences. They all share an interest in the practice of experimentation. But how can simplistic philosophical or sociological models help us to understand complex historical cases? Here we might turn to Hecht once again: "Even in the best case," he explained while defending the use of mathematics in biology, "the mathematical treatment can never be as complex as the organism is in reality." Analogously, it would be pointless to expect philosophical or sociological models to describe historical processes in detail. They are valuable for historiography precisely because they are simplistic and abstract. They can enrich historical analyses, just as mathematical models can, according to Hecht, further the study of complex organisms:

> The simpler and the more concrete a model is, the clearer one can be about its relation to the organism and the more direct are the experiments which can be carried out in expressions of it. Their deviations from observed facts then become clear and can be used as the starting point for new ideas and new experiments.[33]

Thus, the simpler (fewer assumptions) and the more concrete (specific assumptions) a model is, the clearer its asserted implications are for experimental practice, and the more directly can we analyze historical events in terms of the model. Situations in which we find actual scientific practice to diverge from philosophers' or sociologists' expectations offer exciting starting points for future studies in the history of the life sciences.

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[31] Hecht became the protégé of Jacques Loeb (1859–1924) and continued to work on the photochemistry of vision. He received several National Research Council grants, and Columbia University created a professorship for him (thanks to Thomas Morgan's efforts). Scott-Moncrieff's work, in turn, was celebrated by Haldane 1937, on 4, "as a model for future researches." Haldane speculated that initiating Scott-Moncrieff's project may have been his "most important contribution to biochemistry." According to Meunier 2020, physiological genetics "constituted one of the most significant new styles of thought and practice in genetics in the interwar period."

[32] Anthocyanins were studied, for instance, by Kenneth Thimann and Yvette Hardman Edmondson (1949) at Harvard University and Felix Mainx at the German University in Prague; see Felix Mainx to Hans Thirring, 7 May 1946, Nachlass von Hans Thirring (1888-1976), Österreichische Zentralbibliothek für Physik, Vienna, B 35–1606. Hecht's former student George Wald (1933) studied rhodopsin in collaboration with the organic chemist Paul Karrer (1889–1971) and the physical chemist Fritz Weigert (1876–1947); see George Wald Papers, Harvard University Archives, Cambridge, Mass., HUGFP 143, box 10, folder "Paul Karrer," and box 22, folder "Weigert, Fritz."

[33] Hecht 1931, on 289. Translation is mine.

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