"Evolution and Tinkering" (1977), by Francois Jacob

In his essay "Evolution and Tinkering," published in Science in 1977, François Jacob argues that a common analogy between the process of evolution by natural selection and the methods of engineering is problematic. Instead, he proposes to describe the process of evolution with the concept of bricolage (tinkering). In this essay, Jacob does not deny the importance of the mechanism of natural selection in shaping complex adaptations. Instead, he maintains that the cumulative effects of history on the evolution of life, made evident by molecular data, provides an alternative account of the patterns depicting the history of life on earth. Jacob's essay contributed to genetic research in the late twentieth century that emphasized certain types of topics in evolutionary and developmental biology, such as genetic regulation, gene duplication events, and the genetic program of embryonic development. It also proposed why, in future research, biologists should expect to discover an underlying similarity in the molecular structure of genomes, and that they should expect to find many imperfections in evolutionary history despite the influence of natural selection.

The author of the article, François Jacob, studied enzyme expression and regulation in bacteria and bacteriophages at the Institut Pasteur in Paris, France. In 1965, Jacob won the Nobel Prize in Physiology or Medicine with André M. Lwoff and Jacques L. Monod for their work on the genetic control of enzyme and virus synthesis. At the Institut Pasteur, Jacob and his colleagues constructed a model of gene regulation according to which regulatory proteins in cells interact to switch on or off genes, and thus control physiological processes. They named this regulatory mechanism an operon, and hypothesized that it existed in the cells of all living organisms. Subsequent research confirmed their hypothesis. The ubiquity of regulation processes found at the molecular level led Jacob to consider its implications for evolutionary biology.

Jacob was also influenced by the work of Claude Lévi-Strauss, who was affiliated to Collège de France in Paris, France, and who applied the theoretical framework of structural linguistics to anthropology. Lévi-Strauss argued that researchers could analyze human communication through the various relations between the signifier and the signified and the changes in the relations between these units. In a similar way, Jacob said that the study of evolution could benefit from the analysis of the main units in molecular biology, such as the structural genes and the regulatory genes, and from the analysis of the changes in the relations between the units involved in the regulation of cell physiology. In his 1977 essay, "Evolution and Tinkering," Jacob assimilated his knowledge of molecular biology into his philosophical ideas about the nature of science and scientific method.

The essay has ten sections. Jacob begins with an outline of his conception of the scientific worldview and the relationship between the natural and social sciences. In the first two sections, Jacob states that science is a human product that consists of a series of cultural attempts to delimit the possible by framing explanatory systems and bestowing unity and coherence upon the world. Like mythology, science attempts to explain the actual by delineating the possible, including the unknown or the invisible. Science, Jacob claims, can be differentiated from other cultural myths by its commitment to experimentation, and its ongoing process of criticism and revision. As such, science aims to provide only partial and provisional answers to questions about the world. The history of science, according to Jacob, depicts a pattern in which scientific knowledge begins as isolated pieces of knowledge in particular scientific domains, and develops into a unified account of phenomena.

In the third section, "The Hierarchy of Object," Jacob addresses the challenges of studying objects, such as living organisms, human language and behaviour, and social and economic structures. Jacob argues against what he calls methodological reductionism, stating that it would be absurd to try to explain something complex, like democracy, by appealing to the structure and properties of its

elementary physical particles. Nonetheless—Jacob notes—the laws that govern elementary physical particles constrain every higher level object of study, including political structures. Lower levels of the hierarchy of objects limit the range of possibilities for objects in higher levels.

In the fourth section, "Constraints and History," Jacob states that most objects of scientific study are complex organizations or systems influenced by a combination of constraints and history. For instance, he argues that emergent properties of a system can be explained by appealing to the components of the system, but they cannot be deduced from them. In other words, one can not predict the emergent properties of complex systems, like cells' and organisms' properties, from the properties of their components. The complex nature of the objects of study constrains predictions. Thus, such objects require examination at more than one level of analysis. Furthermore, Jacob argues that, because complex objects can result from evolutionary processes, they are also constrained by history. For example, scientists have shown that the structure of a cell relies on its molecular elements and composition. However, Jacob notes, any evidence of these molecular elements in prebiotic time is not sufficient to explain the origin of life on earth. Historical conditions, including highly contingent events, have played a role in the origin of life.

In the next two sections, Jacob introduces and develops the metaphor of tinkering to bring into focus the historical character of evolutionary theory. Jacob begins, in the fifth section, by describing the process of natural selection as an imposition of constraints on open systems, or organisms. Natural selection, according to Jacob, is both a negative and a positive force. It is negative in the sense that it works to eliminate less fit variants in a population, and it is positive in the sense that it works to integrate mutations that accumulate over time to produce adaptations. Jacob states that natural selection's creative force is evident in its ability to recombine old material into novelties; new structures, new organs, and even new species.

In section six, "Evolution and Tinkering," Jacob dismisses a comparison between natural selection and engineering for three reasons. First, unlike natural selection, an engineer works according to a pre-conceived plan of the final product. Second, an engineer actively chooses her materials and has access to the best tools designed for accomplishing the task at hand. Natural selection, in contrast, affects the structurally and functionally imperfect parts of the biotic world and reconfigures existing systems into novel ones. Third, if the engineer is successful, the final product achieves a level of perfection. Evolution by natural selection, however, yields imperfect products. For these three reasons, Jacob rejects an analogy between natural selection and engineering, and instead he proposes the metaphor that natural selection is like a bricoleur (tinkerer). Like natural selection, a tinkerer works with no specific end in mind, collecting any materials at his disposal, and rearranges them into a workable object. Thus, contingency constitutes the main feature of evolutionary processes.

Jacob further elaborates this analogy in the seventh section, "Evolution as Tinkering." Different tinkerers, Jacob argues, likely develop different solutions to similar problems. For example, evolution has resulted in different types of eyes—pinhole, lens, and multiple tubes—to address the issue of how organisms use light to perceive the world. In these cases, natural selection used materials at its disposal to form differently-structured adaptations to similar problems. Here, Jacob underscores the claim that evolution never produces new forms from scratch.

Jacob argues that this tinkering characteristic of evolutionary processes is most evident at the molecular level. In section eight, "Molecular Tinkering," he explains that all living organisms, both unicellular and multicellular, exhibit an underlying unity in their chemical structures and functions. Jacob states that, because all life shares the same organic molecules and similar metabolic pathways, it is more probable that new functional proteins have arisen from a rearrangement of genetic elements than it is that those proteins appeared anew. As evidence, Jacob cites the discovery that similar DNA sequences from organisms as distantly related as fruit flies and pigs help cause structures as different as wings and legs to develop.

To support his analogy, Jacob appeals to a hypothesis of Susumu Ohno's, who worked at City of Hope Medical Center in Duarte, California. Ohno presented the hypothesis in 1970, and it is about the logic of gene duplication events in evolutionary history. When a gene gets copied or duplicated in a genome, the new gene lacks the functional constraints of the old gene. In such cases, the

duplicated copy can accumulate beneficial or neutral mutations with little deleterious effect on the overall fitness of the organism. This accumulation can lead to the re-arrangement of genetic elements, so that existing structures can acquire new functions. This hypothesis of genomic change, Jacob argues, illustrates the process of tinkering.

According to Jacob, molecular biologists have shown that most morphological change in vertebrates has not resulted from new structural genes, but rather it is the consequence of a change in the regulation of genetic components, including events like heterotopy, a change in the spatial location of developmental events, and heterochrony, a change in the timing of developmental events. Jacob argues that these events occur in embryonic development according to the precise schedule of a genetic program, suggesting that gene regulation is the key factor in the generation of animals' forms and functions.

In the ninth section, Jacob outlines two consequences of the metaphor of evolution as a process of tinkering. First, if his analogy holds, then biologists should expect to find similarities in the underlying molecular elements of different species. For example, Jacob argues, biochemists have discovered hormone peptides that trigger a variety of chemical reactions in cells from organisms in different species. Second, biologists should expect to see many imperfections or redundancies in the design of organisms. For instance, Jacob explains, the human reproductive system illustrates a less than perfect mechanism in which almost half of the total number of conceptions result in no viable fetuses.

Jacob ends his essay with a final example of tinkering, arguing that the human brain is a product of highly contingent, historical events. Jacob contends that, in humans, the addition of the neo-cortex to the rhinencephalon, a primitive part of the brain responsible for the sense of smell and theorized to control instinct, has set the conditions for the evolution of the human brain. The human brain is thus the result of an imperfect patchwork of a structure controlling visceral or emotional drives, the rhinencephalon, and a structure controlling more sophisticated cognitive abilities, the neo-cortex. This case can be extrapolated, Jacob argues, to a general rule for evolution: evolution is the net result of a particular sequence of historical opportunities.

Jacob's essay had, at first, a mixed reception. Many biologists said that the description of evolution by natural selection as a process of tinkering was blatantly obvious. In 1983 Walter Gehring and his team at the University of Basel in Basel, Switzerland, discovered of a standard set of DNA sequences called the Homeobox in genes that controlled the embryonic development of body plans of animals. Scientists soon found the Homeobox in genes of diverse organisms from flies to humans. Given those results, scientists explicitly began referring to Jacob's essay and to his concept of tinkering.

In 1982, Jacob published a series of lectures given at the University of Washington in Seattle, Washington, under the title The Possible and the Actual, which includes a slightly modified version of his original essay, "Evolution and Tinkering," as well as some essays expounding his philosophy of science. In 2006, the Novartis Foundation in London, United Kingdom, held a symposium on the concept of tinkering in evolution and development. By the second decade of the twenty-first century, scientists had cited "Evolution and Tinkering" thousands of times.

Sources

- 1. Artmann, Stefan. "Four Principles of Evolutionary Pragmatics in Jacob's Philosophy of Modern Biology." Axiomathes 14 (2004): 381–395.
- 2. Carroll, Sean B. Endless Forms Most Beautiful. New York & London: W.W. Norton & Co., 2005.
- 3. Jacob, François. "Evolution and Tinkering." Science 196 (1977): 1161-1166.
- 4. Jacob, François. The Possible and the Actual. Seattle: University of Washington Press, 1982.
- 5. Laubichler, Manfred. "Tinkering: a Conceptual and Historical Evaluation." In Tinkering: The Microevolution of Development, Novartis Foundation Symposium 284. New York: John Wiley, 2007: 20–34.
- 6. Lieberman, Daniel E., and Brian K. Hall. "The evolutionary developmental biology of tinkering: an introduction to the challenge." In Tinkering: The Microevolution of Development, Novartis Foundation Symposium 284. New York: John Wiley, 2007: 1–19.

- 7. McGinnis, William, Michael, Levine, Ernst, Hafen, Atsushi, Kuroiwa, Walter, Gehring. "A conserved DNA sequence in homoeotic genes of the Drosophila Antennapedia and bithorax complexes." Nature 308 (1984): 428–33.
- 8. Morange, Michel. "French Tradition and the rise of Evo-devo." Theory in Biosciences 126 (2007): 149-153.
- 9. Nobel Prize Foundation. Nobel Prize in Medicine or Physiology 1965. http://www.nobelprize.org/nobel_pri/1965/ (Accessed 16 March 2014).
- 10. Ohno, Susumu. Evolution by Gene Duplication. New York: Springer-Verlag, 1970.