"The Origin and Behavior of Mutable Loci in Maize" (1950), by Barbara McClintock [1]

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"The Origin and Behavior of Mutable Loci in Maize," by Barbara McClintock, was published in 1950 in the *Proceedings of the National Academy of Sciences* [2] *of the United States of America*. McClintock worked at the Cold Spring Harbor Laboratory [3] in Laurel Hollow, New York, at the time of the publication, and in the article she describes her discovery of transposable elements in the genome [4] of corn (*Zea mays* [5]). Transposable elements, sometimes called transposons or jumping genes [6], are pieces of the chromosome capable of physically changing positions along the chromosome. "The Origin and Behavior" explains the mechanics of development that occur in maize kernels, which are plant embryos.

In her paper, McClintock explains phenomena in maize kernels that Rollins Adams Emerson, who worked with McClintock at Cornell University [7] in Ithaca, New York, had observed while he was a professor at the University of Nebraska in Lincoln, Nebraska. In the 1910s through 1920s, Emerson conducted maize breeding experiments in which he observed that the maize kernels, which are progeny of the parent plants, showed some unexpected brown and purple spots on a creamy (colorless) background. Emerson hypothesized that the unexpected colors likely resulted from genetic mutations.

McClintock expanded on Emerson's initial work, and she provided evidence and an explanation for what caused the unusual kernel colors, also called the kernels' phenotype. McClintock did not cite Emerson's research in "The Origin and Behavior," but scientists acknowledge his contributions to the study of genetic instability in maize that laid the groundwork for McClintock's research.

Although McClintock did not divide her article into sections, it can be separated into three parts. The first and the last parts of the article serve as the introduction and conclusion, and the research is explained in the central part of the article. In the introduction, McClintock writes about unstable genes [6] observed in fruit flies (*Drosophila melanogaster* [8]). Similar to Emerson's study of maize, Milislav Demerec of Cold Spring Harbor Laboratory [3] had studied unstable genes [6] in fruit flies, finding that certain characteristics such as body color frequently changed, or mutated, in offspring generations. McClintock hypothesizes that the mechanism behind unstable genes [6] in fruit flies and maize is the same.

In the central part of the article, McClintock describes her research on maize. Starting in 1944 she bred different colors of maize kernels and observed the outcomes. McClintock's experiments showed that chromosome breakage and transposition caused the unusual colored phenotypes in maize offspring. Using a staining technique that helped visualize chromosomes under a microscope [9], McClintock observed chromosomal breakage. She notes that chromosomes can physically break and reattach in cells as an organism develops, citing her 1942 article on chromosome breakage in maize. In the conclusion of the 1950 paper, McClintock writes again about similar phenomena observed in *Drosophila* [10]. McClintock presents the similarities between different species as evidence that the mechanism behind chromosome transposition is likely the same in all organisms.

In "The Origin and Behavior" McClintock demonstrates the existence and describes the behavior of transposable elements in chromosomes. After chromosomes break, transposable elements can move along the chromosome and insert themselves into the chromosome at a different location, a process that alters the genes [6] at those locations. McClintock describes two elements that she calls the dissociation (*Ds*) and activator (*Ac*) loci. The dissociation locus is the point on the chromosome where it breaks, while the activator locus activates movement of the transposable elements. When part of the chromosome breaks at a *Ds* locus that affects the kernel's color in maize, the result is unexpected colored spots on the kernel. Thus, McClintock states that the processes of chromosome breakage and transposition cause unexpected phenotypes in maize as well as other organisms. Further, McClintock explains why chromosome transpositions are unstable. In the next generation of offspring, the chromosome may break at the *Ds* locus and transpose again, returning to the wild type phenotype.

McClintock published "The Origin and Behavior" in 1950, and she presented the associated research at a symposium at the Cold Spring Harbor Laboratory [3] in New York in 1951. Historians documented that scientists paid little attention to McClintock's work when it first appeared, and they have debated about the reasons. Some claimed that McClintock's prose is difficult to comprehend, and thus argued that scientists initially ignored McClintock's work because of her poor communication style. Some historians said that because McClintock was a woman performing uncommon research and presenting unexpected results, other scientists did not take her research seriously.

Furthermore, in the 1950s scientists did not expect genetic material to spontaneously rearrange, an expectation that clashed with McClintock's proposal of transposable elements in chromosomes. Some historians claimed that scientists were not ready to accept or understand the discovery of transposable elements because of this preconception. In the 1960s, scientists began to re-consider "The Origin and Behavior" when François Jacob and Jacques Monod [11] in Paris, France, clarified the mechanics of development in bacteria through genetic regulation [12]. In the early 1980s Nina Fedoroff, working in Baltimore, Maryland, isolated and cloned the transposable elements that McClintock had hypothesized. By the early decades of the twenty-first century, scientists had cited "The Origin and Behavior" more than a thousand times: 136 times between 1950 and 1983, and 612 times from 2000 to 2013. McClintock's article documents the discovery of transposable elements and provides an explanation of developmental mechanics for unstable phenotypic variation.

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Subject

McClintock, Barbara, 1902-1992 [20] Chromosomes [21] Transposons [22] Corn [23] Cold Spring Harbor Laboratory [24] Emerson, R. A. (Rollins Adams), 1873-1947 [25] DNA Transposable Elements [26] Zea mays [27]

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