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Sex and the X

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Mammalian sex chromosomes are thought to have evolved specifically to carry sex-related genes. Now, researchers have shown that retrotransposition is facilitating the sex-related gene abandonment of the X chromosome in favor of the autosome.

In January 30 Science, J. Emerson and colleagues at the University of Chicago examined gene movement and observed that a disproportionate number of genes involved in sex determination and function have abandoned the X chromosome, ignored the Y, and relocated to autosomes to function in a male sex-biased fashion. Conversely, genes having a non-sex determining role relocated to the X chromosome (*Science* 2003, **303:**537-540).

"This was really unexpected," Manyuan Long, the team leader, told us. "An excessive number of genes show a trend to avoid being linked to the X chromosome and have evolved new male-specific expression patterns on the autosome. On the other hand, genes move to the X chromosome to avoid anything to do with female sex. There are two directions of gene creation," he said.

In 2002, the team reported unexpected unidirectional gene movement from the X chromosome to autosomes in fruit flies. In this study, the team screened the human genome databases for annotated genes with functional retrotranspositions on different chromosomes and found 94 functional retroposed gene pairs that were not on the same chromosome. Similar screening in the mouse revealed 105 such gene pairs. Their analyses showed that the X chromosome generates an almost 300% excess of retrogenes compared with autosomes in humans, and 305% in the mouse.

"This has raised a lot of new questions," said Long. "When a sex-related gene is trying to abandon the X chromosome for an autosome, what is the point of having the X and the Y? This is completely different to previous speculation."

Charles H. Langley, professor of genetics at University of California at Davis, queries this interpretation and suggests that rapidly evolving genes tend to show male sex bias in their expression. "There is more evidence indicating that genes involved with rapid evolution of the genome are very often associated with male-specific dimorphic traits."

Long believes that the reason for the abandonment lies in part in the X chromosome being present for two thirds of the time in female cells compared with only half the time for autosomes, resulting in 'feminization' of the X-linked genes. Inactivation of one of the X chromosomes during male germ cell meiosis results in X-linked male-specific gene inhibition. Genes, therefore, migrate from the X into autosomes to enable them to function to the benefit of the male.

Rama Shankar Singh, professor of biology at McMaster University, told us that evidence for fewer sex-biased genes residing on the X was well known in invertebrates such as fruit flies and worms. "What this paper does is almost provide a mechanism to explain this," he said.

However, he suggested an alternative explanation: "If a mutation affects a gene controlling some aspect of male reproduction such as fertility or behavior, that gene will be retained because it is under strong selection pressure, and multiple copies will be favored. Stronger selection on male sexual traits

also applies to the differential movement of genes from the X to autosomes, as these are mostly sex-related genes and they are more likely to be retained by natural selection than genes moving in the opposite direction," he wrote in an e-mail to us.

Emerson and colleagues also showed that the X chromosome receives a disproportionate number of retrogenes, but only 14% of these show female expression, compared with 71% in autosomes. This non-sex biased expression may be a result of repression of expression of genes that would have a deleterious effect on females.

"The recruitment issue is more mysterious," said Langley. "That one would need some future analysis and is an approach for more research."

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