siliceous phytoplankton) and diatoms were equally abundant. Biogeochemical signatures of the two blooms such as CO_2 drawdown were comparable, but significantly at SOFeX-N, this drawdown was fueled mainly (60 to 70%) by regenerated nitrogen (ammonium and urea), whereas at SOFeX-S the bloom was driven mostly by nitrate (60%) (*9*). Also, silicic acid depletion was considerably higher at SOFeX-S, because at SOFeX-N (and despite entrainment of silicic acid from surrounding waters) the diatoms were silicic acid–limited (*9*). These differences have important implications for the uptake stoichiometry of carbon, nitrate, and silicon during each bloom.

POC export from the blooms into the deep ocean was measured throughout the experiments. At SOFeX-N, an optical particle interceptor on an autonomous profiler "parked" at 100-m depth recorded the daily export flux for more than 50 days (*10*), whereas at SOFeX-S daily export fluxes were obtained for 28 days using the thorium-234 deficit approach (*11*). Both methods reported severalfold higher export from iron-enriched waters relative to adjacent HNLC waters (*10*, *11*). These export fluxes (*10*, *11*) are the best estimates to date for the Southern Ocean of the ratio of iron added:POC exported. This term is essential to model the impact of elevated iron supply on carbon biogeochemistry during the geological past (*8*), and to estimate the efficacy of oceanic iron enrichment as a geoengineering fix (*7*, *8*). The molar ratio of iron added:carbon exported at 100-m depth was 1.5×10^{-4} at SOFeX-S (*11*), compared to 1×10^{-4} to 1×10^{-5} for SOFeX-N (*10*); both ratios are higher (a less efficient fix) than those previously used by geoengineers in theoretical calculations of carbon sequestration (*8*).

How did the different bloom populations (*9*) impact POC export at each site? At SOFeX-N, export increased between days 30 and 55, resulting in enhanced export of 120 to 1170 mmol C m^{-2} [upper and lower limits assume that the optical "sediment trap" intercepted the particle rain intermittently or continuously, respectively (*10*)], whereas at SOFeX-S enhanced fluxes of 225 mmol C m^{-2} were recorded over 28 days (*11*). However, several issues prevent a direct comparison. The SOFeX-N export event was probably triggered by the subduction of phytoplankton to depth when the bloom filament encountered a front (*10*), whereas no such vertical-transport mechanism was evident at SOFeX-S (*11*). Also, throughout both experiments, phytoplankton exhibited elevated photosynthetic competence F_v/F_m (*9*), suggesting that both blooms were characterized by "healthy" cells, and that they had yet to reach termination by resource limitation (see the figure). Thus, at SOFeX-S, the export flux from the bloom is probably an underestimate (*11*), whereas at SOFeX-N, subduction of "healthy" cells may have prematurely terminated the bloom, and provided an overestimate of export (*10*).

SOFeX has yielded exciting and important findings—in particular, that iron enrichment of low–silicic acid HNLC waters results in a bloom that is dominated by nonsiliceous cells (*9*), which are probably fueled by regenerated nitrogen. Previously it was thought that such taxa exhibited only transient increases in stocks before being grazed by microzooplankton (*12*). Evidence of the fate of the SOFeX blooms was equivocal, with neither bloom exhibiting signs of termination (see the figure). To date, iron-stimulated polar blooms have been observed for periods ranging from 20 to 50 days without evidence of decline, whereas natural polar blooms persist for less than 25 days (*13*) before terminating (see the figure). Such longevity of iron-stimulated blooms may be due to multiple iron enrichments [four over 30 days for SOFeX-N (*9*)], resulting in iron-supply rates considerably higher than occur in nature. Alternatively, artifactual entrainment of surrounding HNLC waters into the iron-enriched bloom may retard algal aggregation and subsequent POC export (*14*). The design of future polar mesoscale iron enrichments must reconsider the magnitude of iron supply, and the spatial and temporal scale of these experiments.

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GENOMICS

Beyond Nature and Nurture

Gene E. Robinson

The horns of a dilemma
are usually on the same bull (*1*).

When it comes to behavior, the nature-nurture controversy has not disappeared. The public is leery of attributing behavioral influence to DNA rather than to the environment and free will; worries abound over the ethical implications of biological determinism. Many social and behavioral scientists are skeptical as well, either because the concept of "DNA as destiny" does not jibe with their understanding of the dynamic nature of behavior or because they consider human behavior to be much more complex than that of animals studied from a genetic perspective. By contrast, biologists have long accepted that genes, the environment, and interactions between them affect behavioral variation. Traditionally, behavioral variation has been partitioned using statistical analysis into genetic (G), environmental (E), and G × E components, an approach that began long before the advent of molecular biology. This retains the flavor of the nature-nurture dichotomy, which influences how research in this field is interpreted. Fortunately, we can now study genes in enough detail to move beyond the nature-nurture debate. It is now clear that DNA is both inherited and environmentally responsive.

Behavior is orchestrated by an interplay between inherited and environmental influences acting on the same substrate, the genome (see the figure). For behavior, gene expression in the brain is the initial readout of the interaction between hereditary and environmental information. Inherited influences ("nature") include variations (polymorphisms) in DNA sequence transmitted from generation to generation over an evolutionary time scale. DNA polymorphisms can affect protein activity (sometimes via posttranslational mechanisms) and gene expression in the brain: when, where, and how much of each protein is produced. The environment ("nurture") also influences gene expression in the brain during the lifetime of an individual (*2*, *3*). Environmental effects occur over developmental and physiological

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time scales. Gene expression in the brain constitutes the first measurable indicator of the interaction between the genome and the environment.

Until recently, this "first phenotype" was not easy to study. However, it is now possible to investigate the relationship between gene expression and behavior in the brains of animal models, thanks to new genomic techniques that make gene expression analysis more sensitive, efficient, and comprehensive. As the following three examples illustrate, we can finally begin to understand the interplay of hereditary and environmental influences on genomic activity and individual behavior. Each example deals with just one gene, but don't be misled. All behaviors are influenced by the actions of many genes; the three highlighted here exert their effects as part of gene networks that give rise to diverse pathways of physiological activity.

The gene encoding the vasopressin V1a receptor plays a prominent part in the social behavior of voles (*4*). The vasopressin system is dynamic in mammals, and surges of this neuropeptide hormone occur in the brains of males after mating. Inherited differences in the brain distribution of V1a receptors underlie striking species differences in vole mating habits. The prairie vole (*Microtus ochrogaster*) is monogamous, whereas most other species of mammal are polygamous. Differences in receptor distribution and behavior are associated with a microsatellite length polymorphism in the promoter of the V1a receptor gene. Transgenic male mice with a prairie vole version of this promoter respond to vasopressin by bonding with females as if they were prairie voles. The V1a receptor gene demonstrates how behavioral variation can be generated by inherited influences on gene expression.

The *foraging* gene (*for*), which encodes a guanosine 3′,5′-monophosphate–dependent protein kinase (PKG), causes inherited differences in behavior in natural populations of the fruit fly *Drosophila melanogaster* (*5*). Allelic differences in *for* expression result in two foraging variants: "Rover" flies have higher levels of *for* mRNA and PKG activity and are more active food gatherers than "sitter" flies. An ortholog of *Drosophila for* is involved in regulating food gathering in the honey bee *Apis mellifera*. In this case, the effect occurs over a developmental, rather than an evolutionary, time scale (*6*). The age-related transition by bees from hive work to foraging is associated with an increase in *for* expression in the brain. Expression of *for* in the bee brain also responds to the dynamic aspects of life in a bee colony, such as when the need arises for some individuals to begin foraging earlier in life than usual. For example, a spike in birthrate that results from favorable environmental conditions in the spring yields a colony deficient in foragers; precocious foragers show a premature increase in *for* brain expression. Likewise, treatment that elevates PKG activity also causes precocious foraging. The *for* gene demonstrates how behavioral variation can be generated by both inherited and social (environmental) influences on the same gene, albeit in different species.

The steroid glucocorticoid hormone is an important component of the system that coordinates behavioral responses to stress in vertebrates. Rats (*Rattus norvegicus*) with a more active glucocorticoid receptor–encoding gene in their brains are more tolerant of stress than individuals producing fewer receptors. These differences explain variation in maternal care exhibited by different mother rats (*7*). Variation in maternal care in rats is inherited; pups that receive the minimum care from their mothers grow up to return the favor when they have their own offspring. Apparently, pups experiencing indifferent care show profound changes in brain gene activity, including decreased expression of the glucocorticoid receptor gene. But these inherited differences in gene expression and behavior occur even in the absence of DNA polymorphisms. In the case of the glucocorticoid receptor gene of neglected rat pups, it is epigenetic modification of the DNA sequence through methylation that is involved in their altered adult behavior (*8*). Hence, environmental influences on behavior can cause epigenetic changes in the genome that are inherited.

Any modern reformulation of nature-nurture questions concerning behavior requires knowing which genes vary as a result of heredity and which genes respond to environmental factors. A broad search for genes sensitive to both influences might provide breakthroughs in the study of genes and behavior. These genes might be pacemakers—evolutionarily labile and mechanistically important—and their identification may lead to molecular pathways that are critical to the brain machinery that modulates behavior. Identification and analysis of the promoters and enhancers that regulate these genes should also provide important insights into how inherited and environmental factors affect brain and behavior.

Emphasizing the dynamic responsiveness of the genome over different time scales not only provides a framework that includes both mechanistic and evolutionary explanations of behavior at the molecular level, but may also attract more social and behavioral scientists to the quest to understand the relationship between genes and behavior. In the past, social and behavioral scientists might have dismissed molecular studies of behavior in animal models by pointing to the greater complexity of human behavior. Yet the examples offered here—pair bonding, foraging, and care of offspring, each involving molecules known to also be present in humans—illustrate complex behaviors performed over days and weeks or even a lifetime. These behaviors have learned components and are performed in a social context. The value of animal models can be further enhanced by applying genomics to generate large-scale expression profiles of individuals with different genotypes tested in different environments (*9*). In addition, the application of informatics should enable new literature-based comparative analyses of behaviors across different species (*10*).

Development of new tools marrying the vast literature on behavior with genomics could also spark increasing involvement by social and behavioral scientists in molecular genetic studies of behavior. This would be a welcome development indeed. A complete explication will require the integration of diverse perspectives in molecular biology, neuroscience, evolutionary biology, and the social sciences. Such a collaboration, grounded in our rapidly increasing knowledge of the dynamic genome, should help everyone get past the dilemma of nature versus nurture. Then we can all focus on both the tremendous opportunities and the challenging ethical concerns related to the study of genes and behavior.

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ASTRONOMY

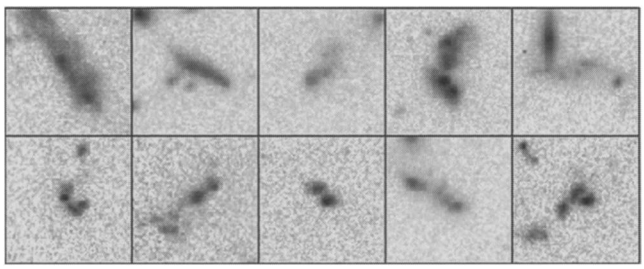
Unveiling the Formation of Massive Galaxies

Christopher J. Conselice

One of the primary goals of modern astronomy is understanding the formation history of galaxies. This problem can be divided into separate subquestions, but perhaps the most straightforward is understanding the formation of the most massive galaxies. There are well-defined predictions for how massive galaxies should form (*1*, *2*), and massive galaxies are the easiest to study because they are usually the brightest at any given epoch. Massive galaxies in the nearby universe contain most of the stars in the universe (*3*) and are generally composed of old stellar populations (*4*). However, it is difficult if not impossible to determine, within a few billion years, the ages of these galaxies with the use of modern methods for dating stellar populations (*4*). The solution is to study galaxies forming in the early universe. This can be done by examining galaxies whose light is highly redshifted and thus emerging from the most distant parts of the universe.

Astronomers are beginning to answer the questions of when and how these massive galaxies formed. Historically, most attention has been placed on determining when massive galaxies formed by identifying and measuring properties of galaxies at high redshift (where larger redshift values z mean that we are looking back at earlier times in the universe; at $z \sim 3$, we are seeing the universe as it was 11 billion years ago). The first samples of high-redshift galaxies, selected by their ultraviolet emission, demonstrated that these systems have number densities and clustering properties similar to those of nearby massive galaxies (*5*, *6*). However, subsequent determinations of the stellar masses of these galaxies (i.e., the amount of mass in a stellar form) showed that these galaxies have lower stellar masses, similar to the mass of the bulge of our own Milky Way galaxy (*7*). Very few if any of these massive systems have stellar masses within a factor of 10 of the most massive galaxies in the modern universe (*7*, *8*).

The total integrated stellar mass density at these redshifts is also roughly a factor of 10 lower than the stellar mass density today (*9*). It appears from these observations, and from the fact that the star formation rate within galaxies remains high until redshift $z \sim 1$ (*10*), that some massive galaxies did not acquire all their mass early. This is consistent with the Cold Dark Matter model for structure formation, which predicts that the most massive objects form gradually through accretion and merging (*1*). Another possibility is that there are galaxies at redshifts $z \sim 3$ that are not identified in ultraviolet-selected redshift surveys because they are made up of old stars or contain large amounts of dust. Both situations create galaxies with red spectral energy distributions that would be missed in traditional ultraviolet-selected surveys (*11*).



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Galactic mergers and acquisitions. Hubble Space Telescope images of galaxies forming by major mergers when the universe was younger than half its current age. These are some of the brightest galaxies found in the distant universe. These images were taken as part of the Hubble Deep Field program and have sizes a few arc seconds across.

It has been argued that populations of these red, possibly old and massive, galaxies have been found at $z \sim 1.5$ to 3 (*11*, *12*). These systems are characterized by rest-frame optical colors similar to colors of nearby normal galaxies, and their clustering and stellar mass properties suggest that they are massive (*13*). The integrated stellar mass density of these galaxies is

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