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Introduction to Mammalian Genome Special Issue: The Combined Role of Genetics and Environment Relevant to Human Disease Outcomes

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A vision for greater use of experimental models to evaluate the role of genetic variability in environmental health and toxicology (Festing 2001) was outlined at the same time as the revolution in genome sequencing of humans and other species was taking place (Lander et al. 2001; Venter et al. 2001; Waterston et al. 2002). The Genes, Environment and Health Initiative established by the US Department of Health and Human Services and the National Institutes of Health in 2006 laid the foundation for investigating the interactions between environmental and genetic underpinnings of human disease by funding development of tools for genetic analysis and exposure biology. Several years later, the landmark study that sequenced the genomes of 15 mouse inbred strains (Frazer et al. 2007) opened the opportunity to link genetic variants to disease traits using the mouse, one of the principal experimental models in environmental health sciences and toxicology. Further analyses (Yang et al. 2007) revealed significant identity by descent between the homozygous inbred strains and the dominant contribution of laboratory derived strains from *Mus musculus domesticus*. New population-based models have been created based on and aided by this refined understanding of mouse genetics (Churchill et al. 2012; Threadgill and Churchill 2012). Many studies have been published in the decade since that demonstrate the value of population-based testing and the power of genetics as an important dimension of environmental health science and toxicology (Harrill and McAllister 2017; Rusyn et al. 2010).

This Special Issue of *Mammalian Genome* highlights a variety of topics broadly unified by the interest in the combined role of genetics and environment relevant to human disease outcomes. Population-based studies aiming to understand the relationship between inter-individual variation and environmental stressors are now being conducted in humans (Daly and Day 2012; Kwo and Christiani 2017), rodents (Rusyn et al. 2010), and other model organisms (Anholt and Mackay 2018). Importantly, many recent studies were designed to

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translate findings in model organisms to human disease susceptibility and draw mechanistic linkages that may help identify individuals who are sensitive to environmental exposures. For example, Jerry et al (Jerry et al. 2018) demonstrate how quantitative trait loci (QTL) identified in studies of susceptibility to mammary tumors in estrogen-treated rats, together with surrogate biomarkers in humans, help explain gene by environment interactions and breast cancer risk posed by environmental xenoestrogens and endogenous estrogens. Anholt and Mackay (Anholt and Mackay 2018) use the model of *D. melanogaster* to highlight the opportunities to study environmental exposures and complex traits in a non-mammalian model organism. Despite major differences in genetic architecture and transcriptomes between flies and humans, the authors posit that the genetic underpinnings of complex traits can be represented as simplified gene networks in *D. melanogaster* on which human orthologues can be superimposed to provide blueprints for subsequent studies on analogous traits in human populations.

Several reviews in this special issue demonstrate the role of inter-individual variability in health and disease associated with infections, lifestyle, and dietary factors. Verhein et al (Verhein et al. 2018) review human, rodent and *in vitro* association studies that identified biologically plausible gene candidates for susceptibility to pulmonary infections and disease severity, as well as how knowledge of these susceptibility factors can aid in novel strategies to prevent and treat disease that contributes to global morbidity and mortality attributed to respiratory infections. Vellers et al (Vellers et al. 2018) used exercise training as a case study of a lifestyle factor that is associated with the individual's genetic makeup. They describe studies in human and animal models that show a significant contribution of genetic polymorphisms, in both nuclear and mitochondrial genomes, in adaptations to endurance and resistance exercise training. Complex interactions between host genetics and other factors in the adverse health effects of environmental diet-associated exposures, such as arsenic, are reviewed by Chi et al (Chi et al. 2018). The authors posit that nutritional status and the gut microbiome may play an even greater role in the individual susceptibility to arsenic-related diseases than host genetic polymorphisms.

Defining the role that genetics may play in the inter-individual variability and disease susceptibility in absence of a specific toxicant or exposure was the focus of two studies in this special issue. Shorter et al (Shorter et al. 2018) investigated the role of genetics, sex, age, and diet on heart size using a population of DO mice. They found a significant genetic effect on heart weight and identified two mechanistically-relevant quantitative trait loci; diet had no significant effect on the heart weight. Balik-Meisner et al (Balik-Meisner et al. 2018) characterized the extent of genetic diversity in a population of Tropical 5D zebrafish and compared observed population genetic variation across species.

A collection of research articles in this special issue provides additional mechanistic insights into the combined role of genetics and environment relevant to human disease outcomes. Argos et al (Argos et al. 2018) studied gene-arsenic interactions in humans using genome-wide SNP data, gene expression, and DNA methylation. Using data from a human cohort exposed to various levels of arsenic, they first identified loci that modify the effect of arsenic on gene expression and DNA methylation phenotypes. Then, using this set of loci, they tested SNP-arsenic interactions in relation to skin lesions, a hallmark characteristic of

arsenic toxicity. This study not only increased the power of GWAS, but also provided critical mechanistic underpinning to the identified susceptibility loci. The interplay between the status of aryl hydrocarbon receptor (AHR), cytochrome P450 1a2, exposure to polychlorinated biphenyls (PCB), and neurotoxicity was explored using genetically-modified mouse models by Klinefelter et al (Klinefelter et al. 2018). The authors were especially interested in the effects of *in utero* exposures and showed that AHR is a modifier of developmental neurotoxicity of PCB, but not for Parkinson's disease. Hoffman et al (Hoffman et al. 2018) used a panel of recombinant inbred rats to further elucidate mechanisms of alcohol toxicity. They used organ-specific gene expression data to identify transcriptional networks that may connect genetic variability and alcohol-associated phenotypes in a tissue-specific manner, an approach that provides mechanistic linkages to gene by environment associations.

Several manuscripts in this special issue explore the mechanisms that may link genetic diversity and effects by focusing on the role of epigenetics. Latchney et al (Latchney et al. 2018) reviewed the hypothesized mechanisms of multi- and transgenerational epigenetic inheritance through DNA methylation and post-translational histone modifications and the potential sources of inter-individual variations and the challenges in identifying these variations. The authors used data from studies of endocrine disrupting chemicals in rodents and concluded that it is difficult to translate rodent studies of these effects to humans. An experimental study by Israel et al (Israel et al. 2018) tested a hypothesis that baseline variability in chromatin organization and transcription profiles among various tissues and mouse strains may influence the outcome of exposure to the DNA damaging chemical 1,3-butadiene. They found that variability in chromatin accessibility across mouse strains only partially explains the variability in gene expression and that variation in the basal states of epigenome and transcriptome may be useful indicators for individuals or tissues susceptible to genotoxic environmental chemicals.

Finally, the utility of population-based studies to environmental health decision-making was considered. Venkatratnam et al (Venkatratnam et al. 2018) explored population variability in dose-response relationships in the liver transcriptional response to the known carcinogen trichloroethylene. They used a large population of CC mouse strains to explore both dose- and genetic background-dependent transcriptional responses. While this study demonstrated how mouse population-based studies aid in assessment of inter-individual variability in toxicological endpoints, it showed that genetic mapping of complex gene-exposure-dose relationships is still a major challenge even in large CC populations. Chiu and Rusyn (Chiu and Rusyn 2018) reviewed a number of published case studies that demonstrate the potential opportunities for improving risk assessment and decision-making by using CC and DO mice, as well as populations of human cell lines. These studies were placed into the context of the steps in the traditional risk assessment paradigm – hazard identification, dose response, and mechanistic evaluation. This review also shows how these data can improve confidence in extrapolating from studies in animals or *in vitro* to human exposures and disease outcomes. Mortensen et al (Mortensen et al. 2018) propose a complementary approach for how the knowledge of human genetic variability may aid in predicting the extent of inter-individual susceptibility to exposures by identifying key initiating events and adverse outcome pathways.

The collective contribution of the reviews and original research in this Special Issue of *Mammalian Genome* provides an updated overview of how genetic models are now being used to understand mechanisms of inter-individual variation in response to multiple environmental factors, as well as challenges that remain to be overcome. Continued investigation of gene by environment interactions in diverse animal models and human populations should lead to novel strategies to prevent and treat environmentally-driven diseases.

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