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A Move Toward Species-Specific Analyses in Behavior Genetics[1]

D. D. Thiessen[2]

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It is essential that behavior genetics move toward a closer association with other biological disciplines and cast its experiments and interpretations within an evolutionary context. In my opinion, behavior genetics has been too preoccupied with the extent of genetic variability and may, in many cases of high heritability, be dealing with genetic junk. The species as a unit of behavioral response, and as the outcome of genetic polishing, deserves more consideration. Adaptation is always the crux of natural selection and offers the best hope of understanding the evolution of behavior and the restriction of genetic variability. Moreover, it is essential to understand the overwhelming significance of regulatory mechanisms of gene action in natural selection and to relate these to behavioral speciation. Examples for these arguments are discussed here.

INTRODUCTION

The study of social behavior in the Mongolian gerbil (*Meriones unguiculatus*) and of single gene effects on behavior in mice (*Mus musculus*) has convinced me that evolutionary theory holds the principal key to the understanding of most behavior. While indeed we may be seeking answers to the right questions—questions about variability, heritability, and gene–environ-

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[2] Department of Psychology, University of Texas, Austin, Texas.

ment interactions—I suspect that our strategies and tactics are often restrictive, if not self-defeating.

One cannot, it seems to me, fully understand genetic variations, mutant forms, and recombinant types without first identifying species-specific behaviors, without first exploring gene flow between natural populations, and without first defining gene relations to environmental adaptation. Nor can one learn the intricacies of artificial selection, balanced polymorphisms, and heritability without first knowing the diversity of environmental demands, the characteristics of isolating mechanisms, and the structure of social systems. Finally, it is nearly impossible to investigate critical physiological processes intervening between DNA action and behavior without reference to the evolution of regulatory genes, gene canalization, and homeostasis, and without an understanding of convergent and divergent evolution. In short, in order to understand the genetics of behavior we must attend to the demands of natural selection and the function of behavior in gene transmission and species survival. Ernst Mayr cast the challenge for behavior genetics when he said,

> There are vast areas of modern biology, for instance, biochemistry and the study of behavior, in which the application of evolutionary principles still is in the most elementary state. (Mayr, 1970, 7)

We must agree, unfortunately, that Mayr is correct and that at best we have given lip service to the importance of evolution in the structuring of behavior. Behavioral evolution has been left primarily to the ethologists, who, in spite of their impressive accomplishments, lack genetic sophistication and an appreciation of laboratory techniques, and species-specific analyses have been the province of comparative psychologists, who for the most part are unconcerned with individual differences and ecological adaptation. Each discipline has of course made experimental and theoretical progress, but rarely have their views been sufficiently broad to include the significant principles of all the separate disciplines. It is the field of behavior genetics, in my opinion, that can forge links between the various disciplines and provide unification within the broad framework of evolutionary principles.

Paradoxically, the very advances that gave behavior genetics its separate character are the same that compel it to search for new directions of accomplishment and propel it in the direction of evolutionary principles. The last two decades were devoted to three major goals: (1) demonstrating unequivocably the influence of gene action on behavior, (2) establishing the validity of single gene and polygene models of behavioral analysis, and (3) convincing other life science areas of the reality and pervasiveness of gene–behavior interactions. The accomplishments are a matter of record and can be ignored only by the foolhardy. Almost every behavior of interest has been demonstrated to have some genetic base (Manosevitz *et al.*, 1969). Mendelian and related analyses do apply to behavior as well as to morphological and biochemical traits. And indices of gene–environment interactions are as plentiful as the number of studies attempted. A bigger task remains, however, and that is the task of relating behavioral observations to ecological and phylogenetic considerations and completing bridges between behavioral and other biological disciplines.

For now, let me consider the areas that appear to deserve and require the most attention and those that should lead us to a better understanding of evolutionary principles of behavior. My first point concerns what I consider to be the present general preoccupation with individual differences and the need to look more at the unity of the species. The second point considers the utility of organizing research around traits that are diagnostic of species and environmental adaptation. Finally, the third point considers available opportunities for the investigation of regulatory processes of gene action. In total, I hope to demonstrate the value of accepting the species as the unit of behavioral analysis and the utility of viewing species-specific behavior in evolutionary terms.

THE PREOCCUPATION WITH VARIABILITY AND THE CONCEPT OF GENETIC JUNK

Clearly, genetic variation in animals is so pervasive that, with the possible exception of monozygotic twins, it is proper to consider that every individual of nearly every species is unique. Electrophoretic studies of proteins bear this out (Mayr, 1970). In *Drosophila* (Lewontin and Hubby, 1966) and mice (Selander *et al.*, 1969), for example, 30–50% of the loci tested were polymorphic for an average of three or four alleles. Even this estimate is conservative, as only about one-third of the amino acid substitutions are electrophoretically detectable. The extreme estimate is that even closely related

Table I. Behavioral Differences in Sibling Species of North American Thrushes (Genus *Catharus*)[a]

Behavioral characteristic	*C. fuscescens*	*C. guttatus*	*C. ustulatus*	*C. minimus*
Breeding range	Southernmost	More northerly	Boreal	Arctic
Breeding habitat	Bottomland woods	Coniferous woods	Mixed tall and coniferous woods	Stunted fir and spruce
Fight song	Absent	Absent	Absent	Present
Hostile call	*beer-pheu*	*chuck-seecep*	*peep-chuck-burr*	*beer*

[a] From Dilger (1956).

species differ in the majority of their genes (Shaw, 1970). Yet, because of gene neutrality, gene canalization, stabilizing selection, and convergent evolution, little of this distinctiveness is ever expressed.

Gene canalization is so restrictive that even sibling species that are reproductively isolated and that presumably differ by a significant number of genes are often similar or identical morphologically. Four species of North American thrushes of the genus *Catharus* (*C. fuscescens*, *C. guttatus*, *C. ustulatus*, and *C. minimus*) are similar enough visually to confuse each other as well as man (see Table I). Nevertheless, a careful analysis of habitat preference and song characteristics substantiates the species designation (Dilger, 1956). A small number of behaviors, in fact, often appear as the major determinants of species specificity and reproductive isolation.

A study of morphologically similar fireflies of the genus *Photuris* further illustrates the diagnostic value of behavior as an index of specificity. At first glance, it appears that only one or a few species of *Photuris* exist, yet Barber (1951) was able to define 18 species on the basis of flash signals that differed in color (yellow, green, or reddish), intensity, frequency, and pattern. Close observation revealed that these species not only varied in communication signals but in habitat preference and breeding season as well. Thus several behavioral traits act to differentiate the species, even though the number of these is no doubt few relative to the amount of imbedded genetic variation.

King and Jukes (1969) have recently argued, in contradistinction to traditional views, that many mutations that differentiate individuals and species are neutral in effect on biochemical activities and that their presence should not be considered as *prima facie* evidence for natural selection. I would further like to add the point that extreme genetic variability is most likely associated with traits with little adaptive value (also see Falconer, 1960). With those exceptions where survival depends on heterozygosity, traits of a critical nature have generally been selected free of extensive variability that might be harmful to their adaptive expression. The variability that we see in the laboratory, therefore, and that which we can manipulate in artificial selection experiments is probably of little immediate relevance and can in some sense be considered genetic junk. This is not to say that variability cannot be the forerunner of adaptability or that the selected phenotype is not of interest, but only that critical aspects of adaptation and species specificity are often devoid of significant variability.

What needs to be stressed instead of the extent of genetic and phenotypic variability is the critical nature of specialized genes—genes that characterize species, genes that lack variable expression, and genes that insure reproductive fitness. In some cases, major adaptive changes are related to simple genetic systems, and often a behavioral change is the most obvious and significant. It is these "switch" genes—genes that specify major adaptive transitions—that demand our attention and promise to provide significant insights into evolutionary processes. For it may be the case, as Ernst Mayr has said, that

> The larger the number of genes that contribute to the shaping of phenotypic trait, a "character," the less likely it is that such a character will be modified through natural selection. (Mayr, 1970, p. 367)

Or, to put it another way, polygenic traits respond slowly to selection pressures, and their change may lag behind adaptive needs. Major gene effects, on the other hand, can be moved to an adaptive level of functioning quickly and fixed at that level in relatively few generations.

Several illustrations point to the crucial nature of switch genes in the modification of adaptive behaviors. The classic analysis is that of industrial melanism in moths (Kettlewell, 1955), where one or two major genes convey cryptic coloring to moths so that they match the darkened and polluted environment. The selection for a dark morph took less than 100 years, and now that industrial pollution is being reduced the light morph is reestablishing itself (Cook *et al.*, 1970). Similarly, the ecdysone-dependent metamorphosis of *Diptera* species (e.g., *Drosophila*) seems to depend upon the activation of a few key genes on loci of chromosomes I and IV (Beerman, 1965). And in the laboratory it has been found that a host of characters leading to adaptation can be grounded mainly on a simple major gene difference. A particularly elegant experiment by de Souza *et al.* (1970) illustrates this point:

> In this instance larvae of *Drosophila willistoni* originally had one place to live in the population cages, the food cups. The environment outside the cups was inhospitable, larvae died of starvation and dehydration. However, the situation was changed in time. Genetic variants appeared that conferred higher resistance to dehydration outside the cups. These larvae had a faster rate of development, needed less food, and preferred a solid dry environment to pupate. The environment out of cups of food, which was a lethal environment, became available for the populations. Mayr (1963) has said that "a shift into a new niche or adaptive zone is almost without exception, initiated by a change in behavior. The other adaptations to the new niche, particularly the structural ones, are acquired secondarily." The larvae able to survive and pupate outside the cups are intolerant of high moist food. The behavior of the larvae, together with their capacity to survive away from food, permitted the population to colonize a new ecological niche. (de Souza *et al.*, p. 185)

A single major gene was found responsible for this transition to a new adaptive zone and led to almost complete reproductive isolation.

Finally, the simple but beautifully designed experiments of Julius Adler (1969) should be mentioned. For the study of chemotaxis in *Escherichia coli* bacteria, a capillary tube containing a solution of a chemical attractant is pushed into a suspension of bacteria on a slide and the number of bacteria attracted is counted. Using this straightforward technique combined with single gene mutants, Adler was able to conclude that the peripheral membrane of *E. coli* contains at least five chemoreceptors which direct movements of

Table II. Behavioral Isolating Mechanisms in Sympatric Populations

Mechanisms that prevent interspecific crosses (premating barriers to gametic wastage)

- A. Differential habitat selection and niche specialization
- B. Assortative mating (homogamy)
- C. Pair formation and internal fertilization
- D. Incongruous social signals
- E. Uncoordinated mating patterns (including seasonal)
- F. Social exclusion
    - 1. Competition for resources
    - 2. Social class differences
    - 3. Territorial barriers

Mechanisms that reduce viability of interspecific crosses (postmating barriers with gametic wastage)

- A. Lack of maternal care
- B. Failure of young to imprint
- C. Agonistic reactions between individuals
- D. Lack of ecological adaptation (including incongruous social signals)

flagella toward different chemical substances. There receptors respond to galactose, glucose, ribose, aspartate, and serine—chemicals of vital interest to bacteria. Clearly, single switch genes are of great significance for the sensory–motor components of adaptation in *E. coli.*

Thus major changes in adaptation can be regulated by one or a few genes operating through species-specific behaviors. Some adaptations are bound to be more significant than others. Whenever we find a large transition in life style, we can be certain that we are dealing with critical genes and genetic junk, and in many cases the number of relevant genes will be small. Those facets of behavioral transition that are likely to be the most informative include metamorphosis from larvae to adult, development of sexual dimorphism, transition from nonflying to flying stages, behavioral selection of different habitats, establishment of reproductive isolation, seasonal variations in behavior, and the evolvement of mimicry. The study of isolating mechanisms in sympatric species, in particular, should be extremely rewarding, as they involve the exaggeration of all aspects of life that preserve the integrity of the species and prevent gametic wastage or maladapted hybrids (see Table II).

So, while I am in accord with the notion that genetic variation is extensive, a prerequisite for adequate adaptation and evolution, and at times essential for survival, I would nevertheless emphasize the importance of investigating simple polymorphic mechanisms that canalize and restrict genetic expression and insure that species uniformity is preserved and that ecological demands are met. The restriction of genetic variation for traits of fitness appears to be the rule rather than the exception.

CONVERGENT EVOLUTION AND THE SUPREMACY OF FUNCTION OVER GENOTYPE

There is little investigative hope of constructing a phylogenetic tree to express the evolutionary trends of behavior. Evolution has not been progressive or linear and has not occurred at uniform rates. In any case, ancestral species are nearly all fossilized or show specializations beyond expectations from phylogenetic relations (Hodos and Campbell, 1969; Thiessen, 1970). There is more hope, it seems to me, in dealing directly with species specializations and treating them as evolutionary reflections of ecological demands. It is in this area of investigation that many mechanisms of behavior are likely to unfold:

> In the case of specialized adjustments, generalizations do not always rest on the invariance of structure–function relations, but rather on the adaptiveness of the response, regardless of genotype or mechanism. Classic Mendelian analyses are hardly relevant to the clarification of control mechanisms, as a near infinite sample of genes and gene products can manage the same solution. Evolution is very opportunistic in the sense that it will take advantage of any genetic variance which will satisfy the same environmental requirement. (Thiessen, 1970, p. 101)

Organisms, without exception, must adapt to variable yet prepotent selection factors such as gravity, climate, food and oxygen supplies, shelter requirements, predators, photoperiodicities, and the like. Clinal variations (variations that are gradated), such as those that show systematic changes with latitude, are especially good evidence for specialized adaptations along ecological gradients. Clines are evident for the majority of continental species and are more apparent in sendentary species that have no alternative but to adapt to environmental demands. For example, as latitude increases in northerly or southerly directions, the following general trends occur in morphology, biochemistry, and behavior:

1. Body size increases (Bergmann's rule).
2. The tail, ears, bills, and limbs become relatively short (Allen's rule).
3. The relative length of hair increases.
4. Wings become more pointed.
5. The relative size of the heart, pancreas, liver, kidney, stomach, and intestines increase.
6. There is a reduction in the pigments phaeomelanins and eumelanins (Gloger's rule).
7. Relative oxygen consumption and metabolic needs decrease, and general activity diminishes.
8. Migratory instincts become stronger.
9. Larger and warmer nests are constructed (King's rule).
10. Home ranges become larger, and territorial behavior is more pronounced.
11. Photoperiodic rhythms become more evident.

None of these "clinal laws" could have been predicted from phylogenetic relationships, but all become obvious when climatic demands are considered. The primary demands are related to needs to conserve body heat, to compete more successfully for limited or seasonal food supplies, and to find protection from predators and changeable conditions of weather. The fact that so many species show these trends suggests that there has been convergent evolution toward those biological features most apt to guarantee species survival around the world.

Convergent evolution, of course, need not be tied to clinal variations. It is often local in character, reflecting the peculiar needs and niche specifications of the species or population. Territorial behavior and scent marking, for example, are evident in at least 13 of the 19 mammalian orders living the world over. In those few species studied to any degree, such as Maxwell's duiker, European rabbit, sugar glider, golden marmoset, golden hamster, and Mongolian gerbil (see Ralls, 1971), it appears that scent marking is related to similar systems of social organization and depends upon an identical hormone

Table III. Examples of Convergent Evolution for Scent Marking

Species	Distribution	Gland characteristics	Behavioral characteristics
Cephalophus maxwelli (Maxwell's duiker)	Central West Africa	Preorbital gland	Objects and conspecifics marked, especially by dominant male
Oryctologus cuniculus (European rabbit)	Europe and North Africa	Apocrine chin gland	Gland and marking more prominent in male and are androgen dependent
Petaurus breviceps (sugar glider)	Australia and New Guinea	Frontal and sternal glands	Gland and marking more prominent in male; used to demark territories and for recognition
Leontideus rosalia (golden lion marmoset)	South America	Sebaceous glands on sternal and gular areas	Gland and marking more prominent in dominant male and become functional at puberty
Mesocricetus aurotus (golden hamster)	East Europe and West Asia	Sebaceous gland on flanks	Gland and marking more prominant in dominant male and become functional at puberty; used to demark territories
Meriones unguiculatus (Mongolian gerbil)	Northeast Asia	Sebaceous gland on ventral area	Gland and marking are androgen dependent and more prominent in dominant male; become functional at puberty; used to demark territories

base (see Table III). Evidently, territoriality acts to conserve basic commodities and is intricately linked to hormones of sex and aggression. In any case, convergent evolution has moved many species toward a territorial system of behavior and has oftentimes capitalized on olfactory signals and reproductive hormones in its regulation. It is evident that in order to understand the function of territoriality we must understand those environmental factors that demand its expression.

Likewise, cryptic shading and coloration, morphological disguises, and warning signals show convergent evolution and local adaptation in innumerable species (Cott, 1940; Portmann, 1959; Wickler, 1968). In all cases investigated, it is apparent that morphology, color, behavior, and background correspond to produce the best possible adaptation for that species regardless of genetic descent. The study of such relations has only begun.

Hence *function* and not mechanism is the key to the understanding of a great deal of convergent evolution, which implies that our attention must be directed toward the outcome of evolution rather than simply toward the genetic structure or physiology underlying a particular phenotype. Obviously, function cannot be completely understood in laboratory investigations where the individual and species stand stripped of their most salient environmental influences. However inconvenient, the behaviorist must move his observational acuity to the geographical site of natural selection and speciation. It is there that the natural adaptations of the species are displayed, and there where relevant laboratory experiments can be formulated.

REGULATORY GENES AND SPECIES-SPECIFIC BEHAVIOR

Higher mammals perhaps have enough DNA for more than 5 million functional genes, yet protein studies would indicate that not more than 10–50 thousand of these are structural genes, genes directly concerned with enzyme formation. Moreover, most of these structural genes are common to a wide array of species and function in approximately the same way. Sturtevant has emphasized the functional equivalence of gene action in this way:

> The more recent comparative biochemical data . . . favor the idea of the great stability of genetic systems, since they show essential identity of some of the gene-controlled basic biochemical pathways in bacteria, fungi, and vertebrates. (Sturtevant, 1965, p. 115)

The near universality of the DNA code itself and the species identity of energy-storing compounds such as adenosine triphosphate emphasize the fundamental identity of life systems.

Although the basic machine of life is similar, of course, its expression shows prodigious diversity, within and between species. Much of this diversity must be due to the modification of basic biochemical processes and not due to differences in chemical forms. In other words, the greatest proportion of phenotypic variance, at least in mammalian species, is probably due to regulatory rather than structural genes—genes that activate, deactivate, or otherwise alter the expression of a finite number of structural genes. Support is added to this view by the observation that the total DNA content of diploid species, which all possess the same fundamental biochemicals, increases substantially and regularly from fish through amphibians, reptiles, and mammals (Britten and Davidson, 1969).

The best-known model for gene regulation is of course that proposed by Jacob and Monod (1961), who determined with the bacterium *E. coli* that the synthesis of galactosidase by a structural gene is under the control of a single regulator gene responsive to the amount of lactose, the substrate of galactosidase, in the cytoplasm. This singularly important observation led to the generalization that gene action is open to modification by environmental factors and hence added the dynamic character to gene action necessary to account for variable expression and homeostatic reactions.

Much behavior that we see may be controlled by regulatory genes open to processes of canalization, early and later experiences, and natural selection. As Britten and Davidson see it,

> Any evolutionary changes in the phenotype of an organism require, in addition to changes in the producer genes [structural genes],[3] consistent changes in the regulatory system. Not only must the changes be compatible with the interplay of regulatory processes in the adult, but also during the events of development and differentiation. At higher grades of organization, evolution might indeed be considered principally in terms of changes in the regulatory systems. (Britten and Davidson, 1969, pp. 355–356.)

Not many clear examples of regulatory actions exist for behavior. We have considered one, the molting pattern of *Diptera* species. Here, under the influence of the inductor hormone, ecdysone, the entire life style of the organism changes abruptly during metamorphosis from that of a wormlike animal to that of a fully developed fly. In our own laboratory, we have found that the territorial scent-marking response of the male Mongolian gerbil is androgen dependent and can be elicited by small amounts of testosterone implanted directly into the preoptic area of the hypothalamus (Thiessen *et al.*, 1968; Thiessen and Yahr, 1970). When genes are prevented from templating RNA by adding actinomycin D, an antibiotic which binds DNA and prevents its action, the hormone implanted in the brain is no longer effective in producing the behavior. Similarly, we have evidence that ribonuclease, which destroys RNA, and puromycin, which disrupts protein synthesis, are also effective in attenuating or blocking the hormone response. Magnesium pemoline, on the other hand, stimulates higher RNA synthesis and to some degree activates

[3] My interpretation.

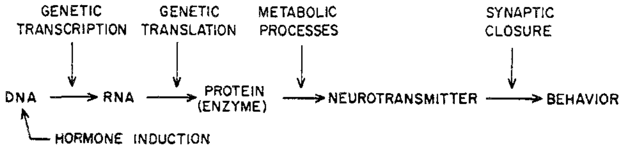

Fig. 1. Hormone–gene flow.

territorial marking and competes with testosterone for receptor sites. Our working model schematized in Fig. 1 supposes that testosterone normally evokes territorial behavior by activating specific segments of DNA, thus initiating a chain of biochemical activities that culminates in territorial marking. Further examination of this model may show that most hormone–behavior relations depend upon gene-regulatory processes, and the concept may extend to many chemical–response relations. Hopefully, such a model is relevant to any concept of environmental determination of gene action and will eventually add a substantial increment to our knowledge of genetic variability and behavior.

In summary, let me stress that behavior genetics is a part of evolutionary biology and that its viability depends upon that relation. While it is theoretically possible to describe gene–behavior associations without reference to their evolutionary origins (and admitting that physiological mechanisms can be studied in the same way), coherence and meaning can only follow when the full implications of natural selection are appreciated. Ultimately, our attention must be on factors that restrain phenotypic variability as well as those that exaggerate it, and those factors that give species their identity. It is necessary, therefore, to emphasize the primary importance of ecological adaptation and concentrate more on regulatory processes that permit differential genetic expression. Above all, it seems to me, the species requires a higher status in our conceptual values as a unit of behavioral response.

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