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(The following was written for a 1991 faculty discussion.)

What can be said about behavioral ontogeny -- for animals in general and humans in particular?

(Note: Nearly every paper or book I have written that deals in some way with behavior, human or otherwise, has significant -- often lengthy -- comments on this topic. But I will start anew here anyway.)

First, it is probably accurate to say that we do not know the complete ontogenetic basis for a single behavior of any organism. This is not surprising. Several decades ago, one of the best-known of all developmental biologists, Charles Waddington, referred to the relationship between the genotype and the phenotype as the "Great Gap" in biology. Thirty years ago, Theodosius Dobzhansky, an equally well-known evolutionary geneticist, stated that "Heredity is particulate but development is unitary. Everything in the organism is the result of the interactions of all genes, subject to the environment to which they are exposed." If true, this latter statement means that we will never know the complete ontogeny for any particular trait of any organism -- behavioral or otherwise -- until we understand the entire ontogeny of that organism. Dobzhansky's (to me, profound) statement means that even if a phenotypic trait is somehow threaded through the entire maze of ontogenetic and environmental influences so as to be expressed eventually in some kind of canalized invariable form, if it is not caused by the entire genome (interacting with the internal and external environment), it is at least properly viewed as being allowed by the entire genome.

This is a bitter pill for every kind of reductionist. Among other things it means that we cannot expect to find one-to-one -- or even several- or many-to-one -- relationships between genetic units and traits. It means that the traits of organisms -- which evolve because the forces of selection are multiple and often entirely independent of one another -- are unrelated or only incidentally related to the particulate nature and structure of the genetic materials: they are produced by the interactions of all the genes. This is more than a bitter pill: it creates a truly dismal prospect, especially for understanding the developmental background of human behavior.

In my opinion most people are either unaware of this problem or in desperation try to ignore it. One way such people proceed is by conflating the question of whether or not genetic variations correlate with behavioral variations -- the so-called "heritability" of a trait (which in fact means the heritability of variations in a trait) -- with the question of the ontogenetic background of a trait. They use the adjective "heritable" to refer to whether or not a trait is predictably expressed as if they meant they actually knew its entire ontogeny, when they know nothing about its heritability in the correct sense of that term because the trait is invariable, so that nothing at all can be said about genetic correlates of its (non-existent) variations. In other words, they misuse the word "heritable" to mean (or imply) that only genes affect the appearance and expression of the trait -- that a behavior is "inherited" or "genetically determined" or "innate." This probably happens partly because the use of heritability is often shortened to "Is that trait heritable?" rather than "Are the variations in that trait heritable?" But it also happens because people are not sufficiently cognizant of the difficulties in understanding the ontogenetic backgrounds of traits or unwilling to accept them.

So what do we do, in the face of Waddington's "Great Gap"? On the general side we try to make sure we do not invoke models of ontogeny that are unacceptable, such as any that imply that a behavior can be "genetically determined" (this cannot be right because the environment always participates). We try not to take easy but erroneous routes, like calling every behavior that has not been observed to vary inherited or innate, because we do not wish our thinking to become stultified or our meaning to be misconstrued. When discussing a specific behavior we try to find out whether or not particular kinds of antecedents affect a behavior -- such as learning experiences or other exposures to environmental variables.

But how do we think about the range of variation in how traits come about during ontogeny? The general statement that traits are always a combination of genes and environment does not carry us very far. It is not satisfying to rely on the dichotomy of "learned" and "unlearned" behavior either. First, we do not have a precise definition of learning. We can talk about different kinds of learning, but we know very little about the adaptive significance of either learning in general or the various forms of learning. Second, we don't know very much about learning until we discover which things are learned easily and which only with difficulty; whether there are changes in this regard with circumstances, age, stage, and other variables; and how and why particular stimuli are instrumental. Third, we don't know what "unlearned" means -- partly because we can never be satisfied that we have tried all appropriate learning circumstances -- so that "unlearned" becomes a negative term implying only ignorance of ontogeny not mechanisms or patterns of ontogeny. If responses to snakes are patterned prior to exposure to snakes, all we can really say is that something other than snakes causes the behavior to develop, not that it is in fact "unlearned" or "innate" or "genetically determined." As a puzzling example, we know that early learning, in novel circumstances that seem to have nothing at all to do with sexuality, can, much later, direct the sexuality of some kinds of birds at a different species, or even at inanimate objects, in ways entirely inappropriate for reproduction. It is mostly an accident that we found this out, and if we had not we probably would have thought of these birds' sexual orientation as unchangeable and called it "innate," "instinctive," "inherited," or "genetically determined."

We generally think of (much or most) behavior as being malleable in ways unlike morphological or even physiological traits, but this is probably an oversimplification. For example, there is some evidence from cladistics that behavioral traits are as useful in phylogenies as morphological traits -- that is, that in a wide variety of organisms their homologies are in general as easily recognizable and traceable through evolutionary time. From comparative study, it is reasonably certain that some particular behaviors, such as copulatory positions in various arthropods, have been unchanged across hundreds of millions of years of evolution (Alexander, 1964).

How does behavior evolve? We usually think of behavior as representing the evolutionarily "pioneering" plasticities or variabilities that enable organisms to get through circumstances that are not entirely predictable ahead of time, therefore are best dealt with by using variously immediate predictors. Thus, an organism with two generations per summer may use the dramatic and highly reliable differences between day length changes in early and late summer to set itself into the particular behaviors (and morphologies) most appropriate to midsummer and winter, respectively (e.g., the field cricket, *Gryllus integer*: Alexander, 1968). Birds use differences in weather, ecological signs, and their own physical condition to adjust their clutch sizes to yield the highest reproductive rate for the season. Humans are evidently evolved to learn to use social circumstances not only to feint effectively in both intellectual and physical combat, but to do such esoteric things as devalue genealogical relatives genetically in ways appropriate to Hamilton's formula for inclusive-fitness-maximizing. In all these cases -- and, I would hypothesize, in all cases -- learning evolves to bring about particular kinds of outcomes in particular situations. This means that if one understood the historical stream of adaptive situations to which any species had been subjected, and the general nature and life niche of the species, he could predict much about the actual patterns of behavior the species would exhibit. Such predictiveness in no way returns us to some version of "genetic" determination of behavior. As a biologist I might in some circumstances be able to predict what action would be taken by a human that I regarded as having the most extreme kind of "free will" of any living thing. That behavior is inevitably "determined" by antecedent circumstances may say something about the physical nature of the universe, and that it can be predicted in many cases may say something about the nature of organic evolution, but neither statement says anything about the "relative" contribution of genes to the behavior or the nature of contribution by genes. I agree with the person who asserted that trying to discuss the relative contributions of genes and environment to a phenotypic trait is like trying to assess the relative contributions of the length and width of a rectangle to its area.

How can we carry further the question of how behavior evolves? Some people have argued that plasticities in behavior -- such as learning -- do not evolve from earlier greater (that is, wider ranges of, or less patterned) plasticities. I think they are wrong, and that particular plasticities probably always evolve from earlier greater plasticities and probably less patterned plasticities (even if in the form of variability we might call "noise"). I hypothesize that the initial plasticity of any trait tends to be (speaking relatively) unpatterned and unspecific (hence, rudimentary and not nearly as adaptive as it might be later, like the seeming "complexity" of a rudimentary acoustical signal that includes many frequencies and not much discernible temporal patterning). Further evolution narrows ranges of plasticity, extends them in one or another direction, produces greater sensitivity to stimuli within particular narrow aspects of the range, and eliminates particular regions on the axis of variability or plasticity. A parallel would be evolving a primitive, variable, and awkward running gait of a quadriped into the more useful combination of walks, trots, and gallops (that's what I mean by selection "patterning" plasticity or variability). Maybe rarely evolution expands ranges of plasticity in multiple directions without doing these other restricting things, but I see that as less common -- even rare.

What occurs next? New rounds of variability appear, and they in turn are narrowed or focused or patterned as above. Such processes continue and continue and continue, leading to ever more extensive and intricate tangles of ontogenetic events and patterns. We biologists can work backward from adaptive expressions of behaviors to get ourselves shallowly into the tangle (even classify the different patterns or "mechanisms" we think we see in the shallow parts of the tangle); we can work forward from the zygote during its early ontogeny to understand how simple things like cell positions and specializations come about; we can even theorize generally about what kinds of events and connections can be involved in the entire tangle. But, practically speaking, we cannot expect, within any version of a "near" future, to unravel the entire tangle -- for any organism or any trait, let alone all organisms and all traits -- and thereby erase the "Great Gap" of which Waddington spoke. For the denser parts of the tangle we can say little more than: don't operate as though either environmental or genetic variables can be ignored. This includes (1) not behaving as though ontogenetic patterning or predictability of behavior means genetic determinism and (2) not assuming that social learning is not evolved to maximize reproduction.

All of that said, what is implied about evolutionary effects on ontogeny by this apparent fact: Among humans, members of the sex that has evolved since antiquity to invest heavily in offspring value more highly in prospective mates evidence of abilities and tendencies to control resources useful to offspring, while members of the sex that has evolved since antiquity to parasitize the parental tendencies of the other sex value more highly in prospective mates evidence of abilities and tendencies to give useful resources to offspring (Buss and Barnes, 1986). The answer to why such things occur today may involve profound sexual differences in psychological mechanisms. Or it may not be so complex after all. Thus, here is a possibly complete answer: Men today are (for whatever historical reasons) bigger and stronger than women, they are willing to use this asymmetry to control resources useful in reproduction, and both sexes know both things. Whether they acquire such knowledge through observational (or other) learning during their lifetimes is not known, but if anyone could find a culture (or a situation) in which females control resources the appropriate test could be conducted.

References

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