Deleuze and West-Eberhard:
The Virtual Status of "Unexpressed Genetic Variation"
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PRELIMINARY NOTE (ADDED 16 DECEMBER 2010)

In this paper I try to bring together two contexts in which the term "gene" is used. Perhaps this is overly hasty. But I'm trying to bring a term from an evolutionary context ("unexpressed genetic variation") together with one from a developmental context ("constructed functional gene").

I was taking off from some thought-provoking lines in Evelyn Fox Keller's *Century of the Gene* (Keller 2000), as when in discussing *eyeless* she writes, "as with so many other eukaryotic genes, the sequence encoding the relevant protein must be constructed post-transcriptionally by splicing. In this sense, the DNA sequence of *eyeless* might be better regarded as a potential gene" (97).

Keller also writes that we might "consider the mature mRNA transcript formed after editing and splicing to be the "true" gene. [JP: As opposed to the DNA sequence as structural or hereditary gene.] But if we take this option (as molecular biologists often do), a different problem arises, for such genes exist in the newly formed zygote only as possibilities, designated only after the fact. A musical analogy might be helpful here: the problem is not only that the music inscribed in the score does not exist until it is played, but that the players rewrite the score (the mRNA transcript) in their very execution of it" (63).

So I may be rushing in where angels fear to tread in bringing these two contexts (evolutionary and developmental) of "gene" together. But if "unexpressed genetic variation" can be seen as potential, as constructed, as only existing ex post facto, at least in a limit case, rather than simply and always as the straightforward way in which the DNA sequence is simply there, waiting to be exposed, then the paper works. If not, it doesn't.

INTRODUCTION

Although the panel theme is a broad one, "Continental Philosophy of Life," I'm going to give a pretty narrowly conceived paper. I'm going to show that Deleuze's notion of the virtual provides an ontological framework for the *potentiality* at work in two key concepts in Mary Jane West-Eberhard's *Developmental Plasticity and Evolution* (Oxford, 2003) namely, "unexpressed genetic variation" and "genetic accommodation."[1]

West-Eberhard's book has garnered a lot of attention in philosophy of biology, which, as we know, is mostly conducted by those who would identify themselves as analytic philosophers. This paper is thus part of an ongoing project in which I seek to show that Deleuze allows some ground for dialogue, some common vocabulary, between analytic and continental philosophers working on the sciences. In a recent article (Protevi 2010) I try to show how Deleuzean concepts can be useful with regard to 4EA cognitive science (embodied, embedded, extended, enactive, and affective). (There's an interesting parallel here. One motto of the 4EA school is "it's not what's in the brain that counts, but what the brain is in." We can substitute "gene" for "brain" here: "it's not what's in the gene that counts, but what the gene is in." What the gene is in is a distributed and differential dynamic system.)

"Developmental plasticity" refers to the way in which organisms of the same species can develop differently in response to different environments. Genetic accommodation entails that some environmentally-induced adaptive phenotypic change is the result of developmental plasticity calling upon previously hidden, i.e., unexpressed, genetic variation to produce new gene expression networks that are then stabilized by natural selection. This unexpressed genetic variation was previously hidden from selection, however, by developmental robustness, the counterpart to developmental plasticity; development is robust in the sense that, given similar environments, organisms in the same species but with different genomes can still produce roughly the same morphology and behavior. The new gene expression networks produced in developmentally plastic individuals can then be selected for, even sometimes in the absence of the environmental stimulus.

I think keeping to this narrow topic is okay for a panel on "continental philosophy of life," however, as West-Eberhard's emphasis on developmental plasticity's role in evolutionary change resonates well with Deleuze's emphasis on the creativity of life over against the self-preservation of the organism, the focus of autopoiesis. Deleuze and Guattari say in *A Thousand Plateaus* that "the organism is that which life turns against itself to limit itself" (ATP, 503). So life as evolutionary creativity limited by the organism is repetition of the same, even if in their more sober moments Deleuze and Guattari admit, perhaps even grudgingly, that autopoietic conservation is the condition of biological creativity: "dismantling the organism has never meant killing yourself.… Staying stratified … is not the worst that can happen" (ATP, 160-161).

DELEUZE'S ONTOLOGY

Deleuze has a tri-partite "ontological difference": in all realms of being (1) intensive morphogenetic processes follow the structures inherent in (2) differential virtual multiplicities to produce (3) localized and individuated actual substances with extensive properties and differenciated qualities. So we have virtual structures, intensive processes, and actual products.

Some concrete examples in the physical, meteorological, and social registers: Deleuze often used Gilbert Simondon's (1995) theory of individuation as a simple model for "actualization." For

Simondon, crystallization is a paradigm of individuation: a supersaturated solution is “metastable” and from that pre-individuated field – which is “differential” in the sense of being replete with gradients of density that do not contain small crystals, but only “implicit forms" or "potential functions" – crystals are individuated via a process of precipitation. The reason crystallization is only a crude image of other individuation processes is that crystals form in homogenous, albeit differential, solutions, while the Deleuzean virtual is composed of Ideas, that is, it involves differential relations among heterogeneous components whose rates of change are connected with each other (Toscano 2006).

For an example of such heterogeneity, let us look at hurricane formation, where there is no central command, but a self-organization of multiple processes of air and water movement propelled by temperature and pressure differences. All hurricanes form when intensive processes of wind and ocean currents reach singular points. These singular points, however, are not unique to any one hurricane, but are virtual for each actual hurricane, just as the boiling point of water is virtual for each actual pot of tea on the stove. In other words, all hurricanes share the same structure, and that structure (the Carnot cycle) also underlies any heat engine (DeLanda 1997).

Finally, in a still more complex social example, Deleuze will interpret Foucault’s notion of “discipline” as an “abstract machine” (another name for Idea or multiplicity) which allows for the increase in productivity with a concomitant diminution in political resistance of any human population. The differential relations here are linkages among rates of change of spatial position, coded movements, complex individual training exercises, and teamwork exercises (Foucault 1977, 167-169). But this abstract machine (which Foucault and Deleuze will call a “diagram”) is incarnated in many different concrete social “assemblages,” such as schools, barracks, hospitals, factories, prisons and so on (Deleuze and Guattari 1987, 530-31 n. 39).

THE DIFFERENCE BETWEEN HEREDITARY AND FUNCTIONAL GENES

There are two basic pictures of biology that most lay people have. The first picture is of evolution by natural selection, which has three factors: variation (from random mutation); heredity (by DNA); and selection (organisms adapting to changing environments). The second picture is of gene-determined development, in which that a contiguous string of nucleic acids codes for a string of amino acids in proteins. By now, these pictures are the subject of vigorous debate, with Piglucci and Müller 2010 presenting the case for the utility of an “extended synthesis” which considerably nuances these ideas: the sources of variation are now thought to include developmental plasticity (and for Lynn Margulis, “symbiogenesis”); heredity is now seen to have epigenetic components; and selection needs to consider “niche-construction” and “co-evolution.”

I’m going to follow Evelyn Fox Keller's presentation in *The Century of the Gene* (2000) where she tries to show that it’s the very progress of molecular biology that has undermined the gene-determined development picture.

Here is the standard picture, which roughly speaking maps onto the slogan “DNA makes RNA. RNA makes protein. Proteins make us.”

1. DNA in nucleus is separated (two strands pull apart).
2. An enzyme (RNA polymerase) copies the bottom strand in complementary mRNA (messenger RNA). This is the process known as *transcription*.
3. The mRNA is transported out of the nucleus into the cytoplasm.
4. On the ribosome, the tRNA (transfer RNA) binds to mRNA by recognizing triplet codons on the mRNA.
5. The tRNA adds an amino acid monomer, correlative to the triplet codons of the mRNA, to the protein polymer chain under construction. This is the process known as *translation*.
6. The protein chain, when complete, drops off the ribosome and goes on to play its role in the cell.

However, we now know that between steps 3 and 4 complex processes of splicing and editing go on. Thus the *primary* mRNA transcript at step 3 has to be edited and spliced to form the *mature* mRNA transcript that goes to the ribosome in step 4.

Why these extra steps? Well, it turns out that proteins sometimes need separated strands of DNA for their synthesis. Often there are big chunks of inactive or "junk" DNA (technically, "introns" for "intragenic region" or "intervening sequence") between the strings of active DNA ("exons" or "expressed DNA"). So the introns have to be cut out (edited) from the primary mRNA transcript and the exons have to be strung together (spliced) to form the mature mRNA transcript.[2]

Another twist: exons can be spliced together in different orders. This is called "alternative splicing." It means you can get more than one mature mRNA transcript from the same primary mRNA transcript (that is, from the same DNA string).

So here's the real process:

1. DNA in nucleus is separated (two strands pull apart).
2. An enzyme (RNA polymerase) *transcribes* the bottom strand in complementary mRNA (messenger RNA).
3. The primary mRNA transcript is transported out of the nucleus into the cytoplasm.
    a. The introns are excised
    b. The exons are spliced together
4. On the ribosome, the tRNA (transfer RNA) binds to mRNA by recognizing triplet codons on the mRNA.
5. The tRNA adds an amino acid monomer, correlative to the triplet codons of the mRNA, to the protein polymer chain under construction. This is the process known as *translation*.
6. The protein chain, when complete, drops off the ribosome and goes on to play its role in the cell.

Thus there is no longer a one-to-one correspondence of DNA sequence and synthesized protein. We have now one gene (DNA string) = many (mRNA transcripts) = many proteins.

Think of it this way: we have to learn to separate the *heredity gene* or *structural gene* (as contiguous string of DNA passed down in reproduction) from the *functional gene* (end-product of transcription processes "forming," from separated strings of DNA, a gene which plays a role in protein synthesis).

And here's the important point: what controls the editing and splicing? *It depends on the state of the cell at any one time*. Thus control has migrated from DNA (structural plus regulatory genes) to the complex system in which DNA plays a (certainly very important) role, but no longer a controlling role.

But the story is not over yet. Not only are different proteins formed from the "same" gene (that is, to repeat, different mature mRNA transcripts can be formed from the same primary mRNA transcript), but proteins function in different ways, according to the cellular context in which they find themselves. This change in protein function is due to changes in their structure; this is known as "allostery." So now we have, instead of "one protein = one function," the case that "one protein = many functions."

So we've gone from "one string of DNA = one gene = one protein = one function" to "one string of DNA (structural / hereditary gene) = many (functional) genes (many mature mRNA transcripts) = many proteins = many functions."

> Of course the first equation is an ideal case: everyone always acknowledged the possibility of errors at each stage (i.e., errors in transmission of DNA in heredity, then transcription or translation errors). Still, the point is that the classic reference point was always a linear, self-contained process by which cell function (and further on, phenotypic traits) could be understood as reducible to proteins produced by genes as DNA strings.
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> So we have to give up the idea that "genes code for traits," and be satisfied with the notion that individual mature mRNA transcripts code for individual proteins (Wheeler 2007). But we can't go simply from hereditary genes (DNA strings) to functional genes (individual mature mRNA transcripts), nor can we go from proteins to traits.
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> We've seen how gene formation and expression depends on cell dynamics which are part of larger networks. (In fact, even the stability of the hereditary gene or DNA sequence is influenced by external events in what's called "stress-induced mutagenesis": in crisis situations, mutation rates increase. This capacity has itself evolved in what's called the "evolution of evolvability.")

But let's talk about development before we talk any more about heredity – anticipating West-Eberhard's views on developmental plasticity as leading the way for evolutionary change.

EPIGENETICS: BEYOND DNA AS “MASTER MOLECULE”

So far we have spoken about individual cell metabolism. But the process of development includes cell differenciation: we have lots of different types of mature cells. Thus gene expression has to follow a temporal pattern.

At first, Keller writes, hopes were high that Jacob and Monod's operon model, which depended on the regulatory vs structural gene distinction, meant that gene expression and hence development could be controlled from inside the genome, by a "genetic program." But now biologists acknowledge the role that *epigenetic* factors play in development.

What are these epigenetic factors? Eva Jablonka and Marion Lamb’s *Evolution in Four Dimensions* (MIT, 2006) presents the case for a most far-reaching picture. Although Jablonka and Lamb present their case in terms of heredity, all these factors are also involved in development (West-Eberhard 2007: 441). Working our way outward from DNA, we note that it is packaged and coiled on the chromosomes. This packaging, DNA and chromosomal proteins together, is called *chromatin*. Chromatin plays an important role in gene expression.

Next we find the *cytoplasm*. In earliest development, the fertilized egg. The chemical gradients in the egg turn out to be very important in development. There are also lots of connections between cytoplasm and chromatin. Control is being dispersed.

This is the most conservative position to take, that epigenetic factors are limited to chromatin and cytoplasm. The most radical thinkers in the Developmental Systems Theory tradition propose other factors, extracellular and even extrasomatic, as long as they reliably recur in succeeding generations (Oyama, Griffiths, and Gray 2003).

But even if we stick to intracellular elements as the limits of our epigenetic factors, we have to recognize that cell position in development plays a role in cell differenciation. Hence gene regulation networks are dynamic and multifactorial; they are no longer simply genomic. Hence development is the key to seeing the limits of genetic determinism.

Instead of DNA as master molecule (as localized and transcendent to the process) it plays a functional role (as immanent to the distributed process). DNA is part of networks that are dynamic and that themselves change over time throughout the development process (which we can see as lifelong, as involving different rhythms).

WEST-EBERHARD’S “ECO-DEVO-EVO” APPROACH

We’re going to focus on Mary Jane West-Eberhard, *Developmental Plasticity and Evolution* (Oxford, 2003). West-Eberhard calls her work "developmental evolutionary biology," which we can call "devo-evo, as opposed to the more well-known “evo-devo” (DPE, vii).

In West-Eberhard's view, evo-devo has had a genetic / molecular focus: how have regulatory gene networks evolved? The breakthrough toward evo-devo came when researchers found that key parts of the genome of many organisms are, in a widely-repeated phrase, "conserved over vast periods of time and shared by widely divergent phyla." A big discovery was homeotic genes, which structure development, acting as genetic switches controlling transcription factors regulating gene expression (turning them on and off). They are essential in body plans and are expressed in the order in which they are found in the chromosome; they control body segmentation, for instance. They are found in many different orders, conserved from before arthropod / mammal division. A famous one is "eyeless." When transplanted from a mouse into a fly, it induces an eye formation. But here's the catch: the eye that forms is a fly eye. It's the fly context that determines what kind of eye is formed (Carroll 2005).

But, W-E asks, in seeking to broaden the molecular focus of evo-devo, what about the organism? After all, there are many ways to skin the developmental cat: organisms are plastic, meaning that they can produce many different phenotypic expressions in response to different environments even with same genetic makeup. In other words, development is *flexible*. But it is also *robust*: even with different genetic makeup, organisms still follow similar developmental pathways.

So if diverse organisms share genes, what is the source of their diversity? The answer is different developmental networks that change the pattern of expression of the genes. But how do those different developmental networks evolve?

W-E proposes that genetic control mechanisms can be exposed to selection by the phenotypic adaptation of organisms to new kinds of environment. For her, this phenotypic adaptation, what she calls "plasticity," ultimately drives evolution.

W-E has three points to make (DPE, p. 20):

1. Environmental induction is a major initiator of evolutionary change (genes are followers, not leaders.)
2. Evolutionary novelties result from reorganization of preexisting phenotypes and incorporation of environmental elements (novel traits are not de novo results of mutation).
3. Phenotypic plasticity can facilitate evolution by immediate accommodation and exaggeration of change (phenotypic plasticity is not mere noise obscuring genetic patterns).

In other words, *DPE* is a book on developmental evolutionary biology – that is, evolutionary biology with reference to development – thus paying attention to "variation and selection w/in populations, speciation, developmental plasticity, and the origin of behavioral, physiological and life history traits" (DPE, vii).

W-E does not deny natural selection, but claims it will favor the spread of a particular environmentally-induced phenotypic variant when it has positive effects on individual fitness, that is, when it is adaptive. With her emphasis on environmental factors we can add an “eco” and call her position “eco-devo-evo.”

Now you may want me to stop right here, because this sounds Lamarckian. It's not though, W-E emphasizes, because there is no direct influence of environment on genotype (DPE, 192). In other words, Lamarck thought that adaptive phenotypic changes were the source of variants that could be inherited (in contemporary terms, adaptive phenotypic changes produce genetic variation). But that's not West-Eberhard's scheme. What she says is that some adaptive phenotypic change is the result of developmental plasticity calling upon previously hidden, i.e., unexpressed, genetic variation (DPE, 437). In other words, neither the phenotype nor the environment produces genetic variation.

The key concept for West-Eberhard is "genetic accommodation" (DPE, 147-57).

The process goes like this: a new phenotype develops (developmental plasticity) by being induced via a genetic mutation or an environmental difference. What has happened here in the latter case is that the new environment has brought forth an untapped *potential* of the pre-existing genetic variation.

This is a key assumption of W-E's argument: unexpressed genetic variation that was previously screened from selection by developmental robustness, that is, the fact that there are many genetic pathways to the same phenotypic expression. It makes sense given our previous discussion that not all genetic variation is expressed; remember that genetic expression depends on cellular / environmental conditions. We have to also remember that such unexpressed genetic variation can be inherited, but that's okay, given gene interaction and piggy-back genes: lots of genes can get inherited without being selected for – this is only a problem for gene selectionists.

The key and controversial assumption is that this new phenotype is adaptive. The notion of adaptive phenotypic accommodation is called the "two-legged goat effect" (DPE, 51-54) from the example of a goat born with two legs which changed lots of things in its phenotype to survive to reproductive age (though it didn't, in fact, reproduce). The principle is that organisms can adaptively change in response to mutations or environmental changes, and that these adaptive changes can become genetically accommodated (again, this sounds Lamarckian, but really isn't).

This change in phenotype creates new selection pressures (because selection is all about interaction of phenotypes; remember, genetic changes simply keep track of real world interactions). The new phenotype starts to spread (as long as, in the case of environmentally induced change, the new environmental conditions reliably recur).

Then the new selection pressures go to work on the regulatory gene networks of the *pre-existing but unexpressed* genetic variation (again, the “pre-existing but unexpressed” is why W-E is not

Lamarckian). The new selection pressures can cause the spread of phenotypes which rely upon the expression of the previously unexpressed genes, so that it (the new phenotype) can eventually become a fixed expression (that is, the regulatory gene networks can be selected for), even when the original environmental novelty is no longer present.

> If the trait appears without recurrence of the environmental stimulus, there is "genetic assimilation" (going back to Waddington's work). "Genetic accommodation" is the general case in which the trait appears with or without the environmental stimulus. If it occurs only with the environmental stimulus, it's said to be an "environmentally sensitive" trait expression. In this latter case, what gets selected for is, conservatively speaking, the regulatory gene network, or, radically speaking, the life cycle that includes the extended network encompassing the recurrent environmental stimulus and the regulatory gene network.

But here's the key: the unexpressed genetic variation is only a potential to be actualized by the construction of gene expression networks. There's no self-present gene as DNA string waiting to be realized. It's not a possible gene, but only a potential one; it takes the intensive (distributed and differential) dynamic system to create a novel functional gene by splicing and editing, excising introns and bringing together exons.

So, to recap, when an adaptive phenotypic change has a genetic component, the gene expression networks (or more radically, the life cyle) for this adaptive phenotypic variant (gene networks that were only "virtual," that is, only *potentials* of the distributed and differential system working on pre-existing but unexpressed genetic variation) will now be selected (if the environmental change reliably recurs), so these gene networks are thus "followers", as opposed to "leaders" in evolution. Instead of being the sole causal factors, they are often just "bookkeeping."

DEVELOPMENT IN *DIFFERENCE AND REPETITION*

Okay, now I want to turn to Deleuze and make the case that his notion of the virtual provides an ontological framework to enable us to understand the potentiality underlying W-E's notion of "unexpressed genetic variation."

THREE ONTOLOGICAL MODES

As we saw above, Deleuze posits three ontological registers:

1. the actual (organism)
2. the intensive (impersonal individuation): embryological or more generally ontogenetic development
3. the virtual (pre-individual singularities in differential-distributed genetic-somatic-environmental networks).

> In a fuller picture of Deleuze's ontology, we see that the virtual field is composed of "Ideas" or "multiplicities," which are constituted by the progressive determination of differential elements, differential relations, and singularities; what are related are precisely intensive processes, thought as linked rates of change (Deleuze 1994, 182-191).[3] Beneath the actual (any one state of a system), we find "impersonal individuations" or intensive morphogenetic processes that produce system states and beneath these we find "pre-individual singularities" (that is, the key elements in virtual fields, marking system thresholds that structure the intensive morphogenetic processes). We thus have to distinguish the intense "impersonal" field of individuation and its processes from the virtual "pre-individual" field of differential relations and singularities that make up an Idea or multiplicity.
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> The term "Idea" should not be seen in a Platonic sense. So let's pause to clarify that the Deleuzean virtual is non-Platonic, in two senses. First, it is not wholly separated from the actual. Rather, intensive processes "counter-effectuate" the virtual: there is a two-way traffic between virtual and intensive, such that the interaction of intensive processes changes the virtual conditions for future processes. An example here would be a Deleuzean understanding of niche-construction: the actual activities of organisms change the selection pressures for future generations. The ecological web of relations that we describe as "selection pressures" is not ghostly, it is perfectly real, but for Deleuze, it does not have the same ontological status as that of a single individuated act (a predator devouring a prey animal, for instance). Rather, the web is virtual, that is, composed of differential elements, relations, and singularities that are progressively determined so that at critical points in the relation of population changes we can find an event such as a population explosion, or in the opposite direction, an extinction. Second, the Deleuzean virtual realm is not composed of self-identical essences. Ideas are not sets of necessary and sufficient conditions for membership in a group and they are not then instantiated by particulars. Rather, Ideas are "differentiated" as zones of intensity in a "space" of continuous variation. As such, they are "perplicated" or interwoven, and they blend into each other at their edges in what Deleuze calls "zones of shadow" (1994, 187; see DeLanda 2002, 22).

Let's spell out the use of "virtual" here a bit. We recall the difference between functional genes as end-products of the transcription process and hereditary genes as strings of DNA on the chromosomes. In other words, the functional genes are only virtually there – their mode of being is virtual – in the hereditary genes.

They have to be actualized through a distributed process in which regulatory gene networks are activated in "dialogue" with epigenetic conditions (intranuclear: mythelation patterns, chromatin markings; cytoplasmic gradients; "positional information" during morphogenesis [temporal-spatial relation of cells to each other]; and even more, perhaps extra-somatic conditions [a particular ambient temperature controlled by niche-construction, for instance; or more complex "scaffolding" operations including exposure to language and other symbolic systems].

Now all these distributed systems are "differential" in Deleuze's sense:

1. the elements are defined reciprocally. Thus "a gene" is what it is only in the network of genes [it only codes for a protein because of its relative position in an arbitrary genetic code]; "a cell position" is what it is in a field of cells [there's no absolute space-time co-ordinates at play, only relative cell position]; "a niche" is what it is only in the network of niches [ecosystems are precisely systems] – or in other words, there is no such thing as "a [single, isolated] gene" or "a [single, isolated] cell position" or "a [single, isolated] niche"];
2. the relations are differential; it's all about linked rates of change: how fast does X element arrive relative to the rate of arrival of Y? Deleuze calls this a delta X / delta Y relation, which is only given determinate values in the actualization process;
3. and the relations contain singularities as remarkable points or thresholds for qualitative change. Singularities as thresholds means the functional genes are "multiply realizable" / divergent actualization from the same DNA string: remember instead of "one string of DNA = one gene = one protein = one function" to "one string of DNA (structural / hereditary gene) = many (functional) genes (many mature mRNA transcripts) = many proteins = many functions."

So one connection of Deleuze and biology is to propose virtuality as the ontological status of functional genes relative to structural genes. What shows up at the end of the transcription / translation process is not a mere tracing of a pre-existing form; it is a genuinely creative process that integrates a differential field. It's more like hurricane formation than following a blueprint.

A PRESCIENT CRITIQUE OF GENETIC REDUCTIONISM

Deleuze insists on the primacy of individuation over differenciation. Differenciation is the production of new species, while individuation is the production of new individuals. This is roughly speaking, the equivalent of W-E's emphasis on developmental plasticity leading the way to evolutionary change.

Following Simondon, Deleuze will distinguish the *field* of individuation (the egg or "metastable field") from "dramatization" as the *process* of individuation (morphogenesis or embryonic development). So both the field and the process are "impersonal," whereas the virtual / differential-distributed genetic-environmental system is "pre-individual."

Deleuze writes that "the nucleus and the genes designate only the differentiated matter – in other words, the differential relations which constitute the pre-individual field to be actualized; but their actualization is determined only by the cytoplasm, with its gradients and its fields of individuation" (DR 251 / 323).

We have seen what Deleuze is saying in Keller's description of the movement away from a genetic program to a distributed / differential network controlling development. The Deleuzean

principle of critique is to outlaw a "tracing" relation between transcendental and empirical or between virtual and actual; in effect, Deleuze forces us to realize the irreducible singularity of intensive individuation processes. The lived experience of the embryo, its morphogenetic "intensive individuration," its twists and folds, do not resemble either the virtual network of relations among DNA strings and epigenetic factors or the actual structures and qualitatively different cell types of the adult organism.

COUNTER-EFFECTUATION

We've seen the relation of individuation and differenciation and the priority of the former. What about the relation between individuation and differentiation? Can changes in intensive processes change the virtual? Deleuze has to answer "yes" here to avoid the virtual being a Platonic realm of essences.

Concerning the relation between individuation and differentiation, Delezue writes in *Difference and Repetition*: "individuation is the act by which intensity determines the differential relations to become actualized, along the lines of differenciation and within the qualities and extensities it creates" (317F / 246E: "L'individuation, c'est l'acte de l'intensité qui détermine les rapports différentiels à s'actualiser, d'après des lignes de différenciation, dans les qualités et les étendues qu'elle crée.")

Writing a few pages later about the clear and confused nature of intensities, Deleuze tells us that the expression of Ideas in intensities "introduces a new type of distinction into these relations and between Ideas a new type of distinction" (i.e., from the relation of virtual co-existing to relations of simultaneity or succession). He then writes: that "all the intensities are implicated in one another, each in turn both enveloped and enveloping, such that each continues to express the changing totality of Ideas, the variable ensemble of differential relations." He concludes that "each intensity clearly expresses only certain relations or certain degrees of variation. … those on which it is focused when it has the enveloping role" (*Difference and Repetition* 325 F / 252E).

Is there a way in which the selective "focus" by which intensities clearly express only certain relations will itself introduce changes into the realm of Ideas? Is counter-effectuation creative? That is, can one say that experimentation with intensive morphogenetic processes will link together new combinations of differential relations, thereby forming new Ideas? That it will express or determine new potentials of the virtual? That's what I take "determines the differential relations to be actualized" (which I prefer as a translation of "à s'actualiser") to mean in the extreme case of an Event or "emission of singularities": it renders them determinate in the sense of linking together previously unrelated relations. In pushing this interpretation, I want to avoid a Platonism in which the Ideas are already determined and so expression is mere copying of already made linkages of relations.

DELEUZE AND WEST-EBERHARD

Recall how developmental plasticity is the creativity of the phenotype and environment (NOT the genotype and environment). When an adaptive phenotypic change has a genetic component, the regulator gene networks (or more radically, the life cycle) for this adaptive phenotypic variant will now be selected (if the environmental change reliably recurs). Now these accommodated or now newly / creatively expressed regulatory gene networks (again, more radically put, the life cycle provoking the extended system of regulatory gene network and recurrent environmental conditions) were only "virtual," that is, only potentials of the pre-existing but unexpressed genetic variation that is only revealed ex post facto.

Here we see the meaning of W-E's phrase that gene networks are thus "followers" as opposed to "leaders" in evolution. Instead of being the sole causal factors, they are often just "bookkeeping." That is, it's the developmental plasticity and the phenotypic adaptivity (in Deleuze's terms, intensive processes of individuation) that take the lead and bring out previously unexpressed potentials of hereditary DNA, that brings out their potential to form the regulatory gene networks. But here's the crucially important point: the potentiality of the hereditary DNA is not preformationism: there's no present / actual / homuncular / already-determined "unit" or "program" in the DNA that determines the actualization of the potential. The virtual is not "self-determining": it's determined, on the spot, each time, by the individuation process. (That's why Deleuze will say the condition is no bigger than the conditioned.)

It's the individuation process that takes the lead, which has to creatively produce something new into the world. This priority of individuation is what W-E talks about as developmental plasticity and phenotypic adaptivity, and is a perfect example of the reality of creative counter-effectuation.

CONCLUSION

We have seen the strong anti-genetic reductionist views of contemporary critical biology. There is a distributed / differential system of feedback among genes and multiple epigenetic factors guiding development. Deleuze would call the structure of this system a virtual pre-individual field. We've seen how this fits the notion of "unexpressed genetic variation." But not only that: in West-Eberhard's concept of genetic accommodation of environmental induction of novel phenotypic traits as a source of evolutionary potential (DPE 145; 499ff), we have seen counter-effectuation as a reality: we've moved from the intensive to the virtual.

So, we have to see both distributed-differential gene-environment networks as virtual and we have to see genetic accommodation as counter-effectuation, as changing the virtual, as bringing forth previously unexpressed potentials, from intensive processes.

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NOTES

[1] The term "unexpressed genetic variation" also appears in Badyaev 2005 and Young and Badyaev 2007. The related notion of "ectopic expression" (gene expression with no discernible function) is covered in Rodriguez-Trelles et al 2005.

[2] Note that unexpressed DNA can evolve by drift (mutation) and other processes, independent of natural selection. This is because NS only works on phenotypes. (NS is about real world interactions, even if they can be tracked by gene shifts.) The variation in unexpressed DNA can be a reservoir for genetic bases for developmental plasticity, as we will see in discussing West-Eberhard.

[3] Deleuze's discussion of the "progressive determination" of an Idea is expressed in the language of calculus (Deleuze 1994, 171), but this is only for expository reasons. Following DeLanda's discussion (2002, 30-31), we see that considered as pure "elements," rates of change are undetermined, but determinable (dx, dy). As these rates of change are linked, they enter into differential relations, which are reciprocally determined (dx / dy) – this is differentiation as yielding instantaneous rates of change. These differential relations define the "existence and distribution" of the singularities of a vector field, but they are only completely determined as those differential relations and singularities are actualized (values of dy / dx) – this is integration as the generation of trajectories.