ARISTOTLE ON EPIGENESIS

Abstract. It has become somewhat of a platitude to call Aristotle the first epigenesist insofar as he thought form and structure emerged gradually from an unorganized, amorphous embryo. But modern biology now recognizes two senses of "epigenesis". The first is this more familiar idea about the gradual emergence of form and structure, which is traditionally opposed to the idea of preformationism. But modern biologists also use "epigenesis" to emphasize the context-dependency of the process itself. Used in this sense development is not simply the unfolding of a pre-determined sequence of changes specified in advance by the organism's genotype. It is also sensitive to inputs from the internal and external environment, which help determine *in real-time* which of the many potential developmental pathways are actualized during the process. Within this paradigm developing embryos are viewed as dynamic and responsive systems that react to inputs from the internal and external environment 'on the fly'. In this paper I argue that, while Aristotle was an epigenesist in the first sense, he would have rejected epigenesis in the more modern sense. First, Aristotle's model of choice for a developing embryo is the automaton that executes a set of preset movements (*GA* 734b9-13, 741b7-15). The automatons he has in mind are not dynamic AI systems capable of modifying their behaviour on the fly in response to environmental cues but completely deterministic mechanisms whose movements are fixed by their original design. Second, given Aristotle's views about the different kinds of causal powers there are, it looks like only intentional agents endowed with actual decision-making powers could be capable of the sort of plasticity at the core of a more dynamic epigenesis. For that kind of epigenesis requires powers for *alternative* outcomes, and Aristotle is explicit that such powers require rational desires (προαίρεσις) that control which of those alternatives to bring about. If I am right, then he could not have made sense of the idea of a developing embryo (as a non-intentional system) making adjustments to its phenotype on the fly in response to emerging problems and opportunities, given the conceptual resources available to him.

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Two Senses of Epigenesis

In a recent paper Aryeh Kosman draws attention to the fact that Aristotle rejected the ancient theory of preformationism in favor of his own model of epigenesis:

> Aristotle is clear and forceful in his rejection of the notion that the offspring itself must somehow be from the very beginning in the seed of one or the other of its parents (*GA* I.21.729b1ff.). His rejection is made possible by a theory that employs the important concept of power or potentiality - δύναμις - according to which the animal is contained in the seed only in the sense that the seed has the power to produce the animal by a process of what came to be called epigenesis. This paper is primarily a plea for the recognition that Aristotle's theory is through and

through a theory of epigenesis, and an argument about what follows from that fact.[1]

Of course it should come as no a surprise that Aristotle was an epigenesist in the sense that he thought form and structure emerged gradually from an unorganized, amorphous embryo. This much, at least, has become somewhat of a platitude. Perhaps the clearest endorsement of Aristotle's commitment to epigenesis comes at *Generation of Animals* (*GA*) 736a35-b5. There he tells us that the animal's form (soul) isn't acquired *in toto* at the start of development; rather, it comes into being gradually as the process advances. While the early embryo already possesses certain rudimentary nutritive capacities, it isn't until later that it comes to possess the capacity for sensation (the property that makes it an animal), while those features that make it a member of a particular species are not acquired until the end of the process. That is why Aristotle says in that passage that a developing organism does not come to be an *animal* and a *human*, or an *animal* and a *horse*, at the same time; rather, the generic attributes are acquired before the specific ones. This expresses, rather clearly, a commitment to epigenesis. For if preformationism were true, then it would be the case that the fetus comes to be an animal and a human, or an animal and a horse, at the same time; each one would be a human or a horse *from the very beginning*. And since Aristotle thinks that capacities of soul develop together with the parts that execute those functions (e.g. sight develops along with the eye), to say that the parts of the soul emerge gradually also entails that the parts of the body do so as well (for "there is no part of the soul which is not in some part of the body", 734a15). So neither form nor structure pre-exists in the embryo except in potentiality.[2]

But there is a more interesting question that Kosman fails to consider. Modern developmental biology now recognizes two senses of "epigenesis" that give rise to what Alan Love characterizes as "a pervasive ambiguity lumbering around in the literature".[3] In the first place "epigenesis" is used for that familiar idea concerning the gradual emergence of form and structure (the sense of epigenesis that Peck and Kosman have in mind). It is opposed to the view that the complete organism pre-exists in miniaturized form inside the sperm (or egg), so

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[1] Kosman (2010, 149-50). See also Peck (1942 [1990], 144).

[2] See also: *GA* 2.4, 739b34-740a4; 2.5, 741b7-15.

[3] Love (personal correspondence).

that what we call "development" is really just the augmentation of those preformed structures. But biologists also use "epigenesis" to emphasize the context-dependency of the process itself.[4] According to this version developmental pathways are not fixed ahead of time by the genetic program. Rather the genes represent a set of potential pathways. And which pathways are actualized during development is determined in real time as the process unfolds in response to environmental cues (including factors internal to the developing system but external to the genome).[5] On this view, then, all the information to build a new individual is not already contained in the genome from the start. Instead a developing embryo is viewed as a more dynamic and responsive system that reacts to real time inputs from the internal and external environment. I shall call these two senses of epigenesis "Epigenesis-1" and "Epigenesis-2" respectively:

> EPIGENESIS-1: The complete organism does not preexists in inside the seed from the start; rather, form and structure emerge gradually from an unorganized, amorphous seed.
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> EPIGENESIS-2: Development is not simply the unfolding of a pre-determined sequence of changes specified in advance by the organism's genotype. It is also sensitive to inputs from the internal and external environment, which help determine *in real-time* which of the many potential pathways are actualized during the process.[6]

While it is certainly not news to anyone that Aristotle rejected preformationism in favor of Epigenesis-1, it is completely up for grabs whether or not he thought development was "epigenetic" in the sense of Epigenesis-2. This is important because Epigenesis-1 is completely compatible with a rejection of Epigenesis-2. Someone can hold that form and structure emerged gradually from an unorganized, amorphous embryo and yet still think that the

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[4] Müller & Olsson (2003, 114).

[5] Epigenesis in this sense is sometimes characterized as environmentally-induced phenotypic variation (Müller & Olsson 2003, 117).

[6] Of course there is much more to Epigenesis-2 than just this (see Müller & Olsson 2003). In this paper I shall focus exclusively on adaptive developmental plasticity, the ability of an embryo to adjust its phenotype "on the fly" in response to changes in the (internal and external) environmental conditions.

process unfolds according to a fixed sequence of pre-programmed changes. My hunch is that this was in fact Aristotle's view.

There is a swift argument and a more complicated argument for my reading. The swift argument is as follows. In *GA* 2.1 Aristotle compares the process of development to the gradual weaving of a net, an image he borrows from the poems of Orpheus (734a18-20). This clearly points towards Epigenesis-1. But he also goes on to drawn an analogy with self-moving automatons:

> It is possible for *A* to move *B*, and *B* to move *C*, and for it to be like the self-moving automatons. For while at rest the parts of the automaton somehow contain [the movements] in them *in capacity*, so that when some primary external agent sets the first part in motion, straightaway (εὐθύς) the next part comes to be [in motion] *in activity*. (*GA* 2.1, 734b9-13)[7]
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> As the parts [of the animal] are already present in the matter *in capacity*, once the starting-point of motion is acquired they develop in a connected sequence just like the self-moving automatons. And the meaning of the statement made by some natural scientists about 'like making its way to like' must not be understood as saying that the parts of the body move in the sense of changing their location… but in the sense of coming to be *in activity* what they previously were only *in capacity*. (*GA* 2.5, 741b7-15)

This points us towards a rejection of Epigenesis-2. By saying all the parts of the animal are already contained in the embryo δυνάμει, I take it Aristotle means that an embryo already has the capacity to develop those parts,[8] just as the automaton already has the capacity to execute a fixed sequence of movements while at rest. Once the process has been triggered by the external agent, the whole pattern of motions unfolds in a connected sequence. Aristotle's choice of model here suggests that he envisions development as a prearranged sequence of transformations. For the automatons he has in mind are not dynamic AI systems capable of modifying their behavior on the fly in response to environmental cues but deterministic

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[7] All translations are my own unless otherwise indicated.

[8] As Kosman says: "the animal is contained in the seed only in the sense that the seed has the power [δύναμις] to produce the animal" (quoted above).

mechanisms whose movements are fixed by their original construction.[9] The mechanical automaton thus points us towards a model of development where all of the changes are specified in advance by what Allan Gotthelf calls the animal's "internal potential for form".[10]

The more complicated argument for my view, which I develop in the remainder of this paper, draws on Aristotle's theory of causal powers from *Metaphysics* IX. Given Aristotle's views about the different kinds of causal powers, it looks like he thinks only intentional agents endowed with actual decision-making powers could be capable of the sort of plasticity at the core of Epigenesis-2. Epigenesis-2 seems to involve powers for alternative outcomes, and Aristotle is explicit that such powers require something like a rational decision (προαίρεσις) that controls which of those alternatives to bring about. If I am right, then he could not have made sense of the idea of a developing embryo (as a non-intentional system) making adjustments to its phenotype on the fly in response to emerging problems and opportunities, given the conceptual resources available to him.[11]

Aristotle and Epigenesis-2

According to Aristotle's theory of heredity the father's semen contains a set of "movements" (κινήσεις) drawn from a corresponding set of "potentials" (ἀπὸ τῶν δυνάμεων), each of which is a capacity for developing a different part of his body (767b23-26, 768b1-5).[12]

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[9] See *De motu* 701b1-10. I discuss Aristotle's use of automatons as a model for development in Henry (2005).

[10] Gotthelf (2012, 3-44).

[11] This way of putting the point might be too strong, since Aristotle would have likely allowed that animal behavior displays a certain amount of adaptive plasticity (e.g. a lion might alter its course on the fly while pursuing a gazelle in order to avoid unexpected obstacles) even though animals lack "decision" in the technical sense of προαίρεσις. In this case I imagine he would ascribe the plasticity of behavior to the possession of various perceptual capacities, including *phantasia* and certain higher-order discriminatory powers (*to kritikon*) that are at least analogous to rationality. See *DA* III 2, 426b8-472a15 (cf. 432a15-17) and the chapters on ethology in *HA* VIII. This possibility does not affect the argument of this paper since it is unlikely that Aristotle thinks the behavior of a developing animal owes anything to such complex perceptual capabilities. I am grateful to Fermin Fulda for pressing me on this point.

[12] Henry (2006), Henry (2009).

On this model an embryo has, from the very beginning, a set of developmental capacities in virtue of which it is capable of developing a certain shape and form. Following Gotthelf, I shall refer to these capacities collectively as the embryo's potential for form (where "form" is used broadly for what we would call the animal's phenotype). Our question is about how much of the animal's phenotype Aristotle thinks is specified in advance by this inherited potential for form. As a working example consider the account of spurs and talons from *PA* 4.12 (694a9-28). Aristotle tells us that some of the heavy birds have spurs on their legs for protection to make up for the fact that they do not fly well, while raptors (which are powerful fliers) instead develop talons on their feet. But no bird has both: spurs are unnecessary if you have talons; and talons are an impediment for ground birds since they would get stuck while walking. Aristotle then says:

> It is from necessity that this difference comes about during development. For the earthen effluence in the body becomes useful for aggression: when it flows upwards, it makes either hard beaks or large beaks, while if it flows downwards it makes spurs on the legs or large and strong claws on the feet. But it does not make each of these in different places simultaneously; for were it spread about, the nature of this residue would become weak. (694a23-8 Lennox translation)

By saying that the difference comes about "during development" one could take Aristotle to mean (in accordance with Epigenesis-2) that the potential for form inherited by each type of bird is undetermined with respect to the parts in question, so that all that is specified in advance are *potential* developmental pathways. On this reading it is left open at the start of the process which type of part a particular bird will develop. Instead how the raw materials get used is not determined by the embryo's formal nature until the appropriate stage of development.[13] The challenge for this interpretation is to show that Aristotle actually has the conceptual resources to account for this kind of adaptive developmental plasticity where embryos are able to adjust their phenotypes 'on the fly' in response to novel problems and opportunities that emerge during the course of development. My suspicion is that he does not.

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[13] The most sustained defence of this interpretation in the literature is offered Leunissen (2013). I consider her view below.

As a way into this issue consider how Aristotle conceptualizes development in *Generation of Animals* 2.4:

> Concerning the differentiation (διάκρισις) involved in the formation of the parts this does not occur, as some say, through the natural action of like making its way to like… but rather owing to the fact that the residue of the female is the sort of thing that is potentially like what the animal is by nature, that is, that the parts are present in it potentially, though none of them are there in actuality. Each of them comes to be on account of this cause and also owing to the fact that when agent and patient interact (θίγωσιν) with one another in the way in which the one is active and the other passive… then *straightaway* the one acts and the other is acted upon (εὐθὺς τὸ μὲν ποιεῖ τὸ δὲ πάσχει). (740b12-24)

This passage gives us a glimpse into the basic causal model that Aristotle is working with in the *GA*. According to this model the development of a given part is conceptualized, in accordance with the definition of change from *Physics* 3.1-2, as the actualization or fulfilment of the matter insofar as it is potentially that part. And that change is occasioned by the mutual activation of two correlative powers: (1) a passive power to be transformed into the part, which is rooted in the embryo's matter (cf. *GA* 741b7: "the parts are present in the matter in potentiality"); and (2) an active power to transform the matter into that part, which is a capacity of the formal nature (or generative soul).[14] Now one way to cash out Epigenesis-2 in Aristotelian terms would be to say that the inherited potential for form that governs development includes certain active powers for producing alternative effects depending on the developmental context.[15] So, for example, Aristotle might hold that the potential for form inherited by raptors and fowl includes a capacity to develop spurs *or* talons. Which way that capacity is activated is not specified in advance; rather, it is determined on the fly in response to the teleological demands that emerge from its particular way of life (*PA* 694a9-22).

This last part is something we might expect in the context of Aristotle's theory. Recall that Aristotle thinks animals develop their generic form before their specific form, so that the

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[14] Aristotle associate the active powers of development with the embryo's generative soul — which he identifies with the *nature* of each thing — just after our passage at 740b34-741a3.

[15] Cf. Leunissen (2013, 19), quoted below.

embryo does not come to be a bird and a raptor or a bird and a fowl at the same time (736a35-b5). Rather, the features that make the embryo a raptor or a fowl are not acquired until the later stages of development. This means that the developing bird will not actually be subject to any particular design requirements stemming from any specific way of life until those later stage. So it would make sense for Aristotle to say that whether the particular bird develops spurs or talons isn't determined until later in the process of development, since there is nothing that teleologically necessitates one part or the other until the later stages. (Neither spurs nor talons are *conditionally necessary* at the start.) If this is right, then we might expect Aristotle to say that the embryo's formal nature cannot make the "decision" to produce spurs or talons until those later stages.

The trouble with this reading is that, while Aristotle does recognize capacities for bringing about alternative effects, he argues that such powers are always found "together with reason" (μετὰ λόγου).

According to *Metaphysics* 9 causal powers come in two kinds: rational and non-rational powers (1046a36-b2). Non-rational powers are characterized by two essential features. First, each one is productive of a single effect only with no alternative, e.g. heat is only capable of heating and what is cold can only cool (1046b6-7, 1048a8). Second, the activation of a non-rational power is necessitated by contact with its correlative power under the appropriate causal conditions so that; as soon as these conditions obtain, the power is activated straightaway (εὐθύς) if nothing impedes it (*Metaphysics* 9.5, 1048a5-8; compare the *GA* 2.4 passage above). By contrast rational powers are powers to produce alternative effects, e.g. the art of medicine is productive of health *or* disease (*Metaphysics* 9.2, 1046a36ff.). For this reason, Aristotle says, contact with the corresponding power under the right conditions is necessary but not sufficient to activate it. Instead there must be some further controlling factor (τὸ κύριον) that determines which of the two alternative ways of activating the power occurs, which he identifies as decision (προαίρεσις). For example, the medical art on its own cannot effect any change. The doctor must decide, on the basis of deliberation, whether she wants to heal her patient or make him sicker. Aristotle makes this point in *Metaphysics* 9.5:

> Some things are capable of effecting change in accordance with reason and their powers are accompanied by reason, while others lack reason and their powers are non-rational, and it is necessary for the former to be present in ensouled things

> while the latter are present in both. And with powers of the latter sort, when agent and patient interact with one another in the way in which they are capable, it is necessary (ἀνάγκη) that the one acts and the other is acted upon, while in the former case this is not necessary. For, while all non-rational powers are productive of a single effect only, rational powers are productive of opposites so that one power will simultaneously produce contraries. But this is impossible. Therefore, there must be some other thing that exerts control (τὸ κύριον), namely, desire or decision[16]. For whichever outcome it desires decisively (κυρίως), it will produce this when it is in those circumstances that are appropriate to its capacity and associates with the patient. (1048a2-13; cf. *De anima* 3.9, 433a1-6)

Given this conceptual scheme it is hard to see how Aristotle could make sense of Epigenesis-2. For the plasticity involved would seem to require the embryo to make literal decisions about which of a series of alternative pathways to actualize during its development.

Consider the raptor again. On the version of the reading developed above what a raptor inherits from its parents is a flexible δύναμις for producing talons *or* spurs. Which way that δύναμις gets activated is determined on the fly at the appropriate stage of development in response to certain environmental cues. But we have just seen that a δύναμις for bringing about alternative effects requires some additional factor to control its activation. And on Aristotle's theory this role is played by decision, which is a rational desire to bring about what deliberation has shown to be the best course of action. In that case it looks like Aristotle would have to say that the embryo (or its formal nature) literally decides that it would be better to produce talons rather than spurs given the demands imposed on it by its emerging way of life. For his causal theory doesn't countenance any other (non-rational) controlling factors for determining which way to activate that δύναμις. This gives us a reason to be skeptical of the idea that Aristotle accepted Epigenesis-2.

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[16] These amount to the same thing, since "decision" is defined as a rational desire to bring about what deliberation has shown to be the best course of action (*NE* 3.3). Decision in this sense is the efficient cause of action (in the sense of πρᾶξις), which Aristotle identifies as a single state with motivational and intellectual dimensions (*NE* 6.2).

If all of the powers at work in development are of the non-rational sort (as Aristotle clearly thinks they are), then this leaves little room for the sort of adaptive developmental plasticity that is at the core of Epigenesis-2. First, as we have seen, every non-rational power is productive of a single effect only with no alternative. Second, the interaction with its correlative power necessitates its activation ("when agent and patient interact with one another in the way in which they are capable, it is necessary that the one acts and the other is acted upon"). In that case there is no need for any additional controlling factor; the activation of each power follows immediately from the causal conditions ("when agent and patient interact with one another in the way in which the one is active and the other passive… then straightaway the one acts and the other is acted upon"). If this is right, then the actualization of the inherited potential for form that constitutes development should unfold in a cascading series of automatic changes triggered by the interactions of the various causal powers involved under the appropriate conditions. And that is just what the model of a self-moving automaton leads us to expect.[17]

To close this paper I want to look at a recent interpretation of Aristotle's theory that attributes to him exactly the sort of view that I have argued he could not have entertained.

Nature as Craftsman

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[17] By characterizing the actualization of the embryo's potential for form as a "cascade of automatic changes" I do not mean to suggest that it is a purely mechanical process. A more complete explanation of the process would locate this (efficient causal) account within a broader teleological framework by showing how each of these necessary interactions as well as their overall choreography take place for the sake of the adult form that results from them (*GA* 2.6, 735a36-b8). Thus I agree with Leunissen (see below) that the capacities at work in development are not "blind"; they are goal-directed capacities. But it does not follow that they cannot also be "automated self-regulating principles". (How a process can be necessitated and also for the sake of its end is outside the scope of this paper: see Johnson 2005, Ch. 7.) The question of whether development is "blind" or "for the sake of its end" is a separate issue from the question of whether it unfolds according to a predetermined pattern or whether some changes are determined on the fly in response to environmental cues.

The most extensive defence of the epigenetic reading of Aristotle in the literature is Mariska Leunissen's paper, "Crafting Natures: Aristotle on Animal Designs".[18] Leunissen argues that Aristotle's tendency to depict nature as a tinkering craftsman throughout the biological works is a clear indication of his commitment to what I am calling Epigensis-2:

> At the physiological level, that is, when we translate Aristotle's talk of goal-directed natures into realizations of potentials for form in the manner proposed by Gotthelf..., this means that those potentials have to be equally 'creative' or 'dynamic'. If I am right in assuming that Aristotle's depictions of natures as craftsmen are no mere metaphors, but in fact reflect different causal patterns that underlie animal generation, the potentials for form that guide embryology and the later development of animals cannot be blind, automated self-regulating principles[19]. Rather, they are flexible and complex, and include the capacities to make the best use of extra materials and to respond to emerging problems or possibilities. (Leunissen 2013, 19)
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> This indicates that at least *at the level of embryogenesis*, Aristotle does allow for something like a transformation of species and that his view of development is epigenetic in the true sense of the term. That is, the 'guidelines' for building with which nature works do not predetermine in advance all the changes that need to be made, but rather leave room for nature to make adjustments to animal design 'on the fly,' as the development proceeds. For his theory of natural teleology this means that the underlying physiology must be rather complex and flexible: the potentials for form that guide the realization of those species are dynamic, rather than blind, automated self-regulating principles, as they are shown to be capable of responding to 'unexpected' changes in circumstances. (Leunissen 2013, 29 emphasis in original)

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[18] The main impetus for my own paper came out of conversations with Leunissen on her original draft. It is worth pointing out that I was the one who originally encouraged her to characterize her position in strongly epigenetic terms, as I thought it best captured the main thrust of what she was trying to say.

[19] As mentioned "automated" does not entail "blind" (see note 16 above).

> My reconstruction above of Aristotle's assumptions about how natures 'weigh' the available natural possibilities and choose the best design option for each individual kind of animal shows that many features are not 'preprogrammed' by the definition of the substantial beings of animals. The 'phenotype' of animals develops gradually, as a result of natures not just doing what is necessary, but also doing what is better and best in response to emerging problems and opportunities. (Leunissen 2013, *44* emphasis in original)

On Leunissen's reading, then, the potentials for form passed on in reproduction do not specify in advance all of the natural changes that occur during development. Rather, they leave room for nature to make adjustments to the animal's basic design on the fly as development unfolds. As should be clear by now I am not convinced that this picture accurately describes Aristotle's view.

In the first place none of the examples Leunissen cites in favor of her interpretation commit Aristotle to Epigenesis-2. In each case Aristotle talks about nature making 'modifications' and 'adjustments' to a kind's basic body plan in order to optimize the form of some particular species. But nothing in his analysis suggests that he is thinking of these as real-time embryological responses to novel design problems that emerge only during the process of development. Consider the example of the elephant's trunk (Leunissen 2013, 34). Normally four-footed animals with split toes have feet that provide support for their bodies and a means for transporting food to their mouths. However, given the constraints on the elephant's form, Aristotle says that nature was forced to modify this basic design by doubling up functions on the trunk (*PA* 659a20-30, 34-6). Leunissen claims that in this case the design problems faced by the elephant emerge during its formation, so that nature has to modify its basic body plan as the embryo develops: "In cases like this, nature still realizes all the functions specified by the definition of the substantial being of the animal, but, because of the design-problems that only become clear during the animal's production process, it has to do so in an 'unexpected' way." (Leunissen 2013, 34-5) But there is no reason to think that. While Aristotle clearly thinks nature 'tinkers' with her designs in some sense, nothing he says in that context suggests that he is thinking of these cases in terms of nature making real-time embryological adjustments to the developmental system. In each case he could simply be presenting us with a thought experiment where nature makes certain hypothetical

adjustments to the species original design (like an engineer tinkering with the design of his automaton before setting it in motion).[20] In other words, all of Leunissen's examples are compatible with thinking of the modifications in question as being programmed into the inherited potential for form from the start. Leunissen at least provides no reason to think her own epigenetic reading of those examples is to be preferred.

Leunissen's strongest case comes from her analysis of *PA* 3.2, 663b22-35 (Leunissen 2013, 35-6). There Aristotle tells us that certain surplus "residues" can sometimes get co-opted by nature for some additional purpose during the process of development:

> But, since there is a necessary nature, we must say how the formal nature makes use of things present of necessity for the sake of something. …For the surplus residue of this kind of [sc. bony] body, being present in the larger of the animals, is used by nature for protection and advantage, and the surplus, which flows of necessity to the upper region, in some cases it distributes to teeth and tusks, in other cases to horns. (Lennox translation with modification)

According to Leunissen, these leftover materials are not present because they are necessary prerequisites for the construction of parts that are themselves specified in the definition of the animal's substantial being (they are not conditionally necessary). Instead they are accidental (unforeseen) by-products of other processes that operate through material necessity. Once those materials become available, the nature of the embryo immediately co-opts them to make what Leunissen calls "bonus features", parts the animal could have done without but make it better. Leunissen takes this as evidence of the adaptive plasticity of development; for these surplus materials are accidental and not specified in the original plan for constructing the animal.

But Aristotle need not be thinking of the availability of surplus residue as an unforeseen accident that nature happens to exploit. The text is perfectly compatible with thinking that the

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[20] Leunissen (2013, 31) herself recognizes several examples where Aristotle is speaking about some "hypothetical moment in time" where nature first designed an animal, analogous to the "first creation" of human beings in the *Timaeus*. I see no reason to think that this example is any different. This moment is necessarily hypothetical, since there is no time for Aristotle before elephants existed since species forms are (in some sense) eternal.

use of these materials is something that is also specified in advance by the developmental program. Imagine an expert sculptor who has been making the same statue for the entire length of her career. She knows that she always needs two-thirds of a cubit of clay for the hands. But she also knows that her supplier packages clay in whole cubits, so that it normally turns out that she has one-third of a cubit left over; the surplus is a necessary by-product of how the clay is packaged. Since she is not wasteful, she always plans on that surplus to make the wings on the helmet. In this case the surplus materials are not some unforeseen accident that affords her an opportunity, which she decides *in the moment* to use for the wings. It is something that happens either always or for the most part, and so she always anticipates having some left over clay to make those extra parts. It is something she budgets for in her original design. Aristotle could have have similar in mind at *PA* 663b22-35.

The other worry with Leunissen's reading is the one already mentioned. Given the conceptual resources available to Aristotle, it is difficult to imagine how formal natures could be responsible for making real-time adjustments to the developmental system in the way Leunissen suggests without turning them into rational agents. This gives us a reason to reject her epigenetic interpretation, since Aristotle does not think formal natures make literal decisions about how to realize their ends.

On Leunissen's epigenetic reading Aristotle treats the development of an animal as the actualization of an inherited potential for form that guides the actions of the formal nature in constructing the animal in the way that the blueprints guide the actions of the builder. But (she argues) that potential for form does not completely determine its actions. Instead, just as a craftsman can make adjustments to the blueprint of the house on the fly in response to problems that arise during its construction, animal natures are capable of making real-time modifications to the kind's basic design during the course of its development. In these cases the inherited potential for form only specifies a set of potential pathways. And which of those pathways is actualized during development is 'up to' the animal's formal nature. The key to her reading is the claim that the capacities that guide development are not "blind, automated self-regulating principles"; rather, "they are flexible and complex, and include the capacities to make the best use of extra materials and to respond to emerging problems or possibilities" (2013, 19).

We have already seen that this way of conceptualizing the capacities at work in development (as powers for alternative effects) requires the introduction of a rational agent whose decisions (rational desires for bringing about the conclusion of deliberation) control how those capacities get activated. For Aristotle does not countenance any other kind of non-rational controlling factor that could play that role. Consider what Leunissen says about snakes:

> A quick thought experiment reveals that no blooded animal whose length is out of proportion to the rest of their body would be able to move swiftly with either two or four feet, and in order to remedy that design problem, nature "decided" not to produce feet in such animals. With this information, it would then be possible to formulate a scientific explanation that does not appeal to any conscious intentionality in nature.

If the argument in this paper is correct, then it does not seem possible, on Leunissen's reading, to generate an explanation of this case without ascribing conscious intentionality to nature. Let's look at the example more closely.

Snakes are the only blooded land-dwellers that do not have legs. One reason for this, Aristotle says, is that nature does nothing in vain but always what is best for each substance given the range of possibilities (*IA* 8, 708a9-20).[21] Now, since no blooded animal can move at more than four points of motion (*IA 7*), the most legs a snake could have would be four. In that case giving snakes legs would be pointless, since they could not move very well with only two or four (cf. *PA 4*.13, 696a12-15). So having no legs turns out to be optimal for a snake. On Leunissen's reading the absence of legs in snakes is not something specified in advance.[22] Instead all blooded land-dweller inherits a "flexible" capacity for producing legs *or* their absence. During the development of a snake nature "decides" it would be better not to construct them and so makes the appropriate adjustment by suppressing its activity. But how does this work exactly? Aristotle is clear that, when a capacity includes the potential for bringing about alternative outcomes, there must be some additional controlling factor — which on Leunissen's reading is the animal's formal nature — that makes a decision about

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[21] For my analysis of this case see Henry (2013, esp. 232-3).

[22] Leunissen (2013, 32).

which of those two alternatives to realize. By contrast, I have argued that if all the capacities involved in development are of the non-rational sort, then (p*ace* Leunissen) there is no need for anything else to control their activation. The activation of each power is necessitated by contact with its corresponding power in the right causal conditions.

The Role of the Environment

In this paper I have argued that Aristotle simply lacked the conceptual resources to make sense of Epigenesis-2 without ascribing genuine rationality to nature. This is because he thinks only rational agents endowed with real decision-making abilities could be capable of the sort of plasticity at the core of that theory. At least Aristotle's theory of causal powers does not countenance any non-rational means for determining which of two alternative ways of activating a power occurs. Without this he simply has no way of explaining how a developing embryo (as a non-intentional system) could make real-time adjustments to its phenotype in response to emerging problems and opportunities. One might object here that this argument turns on the assumption that Aristotle's account of generation in the biological works is constrained by the theory of causal powers developed in *Metaphysics* 9.[23] If he is not working within that framework, then we are free to imagine other ways that the developmental capacities of embryos might be context dependent without having to invoke rational decisions as the factor that controls which of several alternative ways of building the animal is realized. One possibility for this sort of non-rational controlling factor (τὸ κύριον) might be the environment itself.[24]

First of all, there is no indication that the biological treatises are not working within the framework of the *Metaphysics* theory of causal powers. On the contrary, the way Aristotle characterizes the formation of parts in the *GA* 2 4 passage ("when agent and patient come into contact with one another in the way in which the one is active and the other passive… then straightaway the one acts and the other is acted upon") is reminiscent of the description of non-rational powers in *Metaphysics* 9.5 ("with powers of the latter sort, when agent and patient interact with one another in the way in which they are capable, it is necessary (*anankê*) that

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[23] Leunissen (personal correspondence).

[24] I am grateful to Mark Johnstone for raising this objection during a presentation I gave at McMaster University (February 2016).

the one acts and the other is acted upon"). So I am not very sympathetic to this objection. But let's look at this alternative a bit closer. The question here is, in cases where the environment does make a difference to how things turn out, what is doing the explanatory work?

In Epigenesis-2 the capacity itself is the intrinsic (καθ' αὑτὰ) cause of the trait in question, while the environment is simply part of the causal conditions that determine how that capacity is realized ('in environment A the δύναμις produces X, in environment B it produces Y'). In this case the δύναμις itself is the efficient cause of the trait, while the environment forms part of the causal background that determines how it operates. Consider *PA* 694a24-7 again. Aristotle tells us that some birds have hard beaks, some long beaks, some talons, and some spurs and that this difference comes about during development. Now suppose these four different parts are the intrinsic objects of a single non-rational δύναμις. According to the current suggestion how that δύναμις is activated depends on certain features of the environment. For example, if the embryo develops in a hot and dry womb the δύναμις gets activated in one way causing the materials to flow upwards and form a hard beak. If the environment is cold and moist, that same δύναμις gets activated in another way causing it to flow downwards to form spurs on the legs. And so forth for the other options. In each case the 'controlling factor' that determines how the δύναμις is actualized will not be a rational decision on the part of some intentional agent but the environmental conditions themselves.

This strikes me as a more promising way of defending the view that Aristotle endorsed Epigenesis-2. The place to look for such a reading would be *Generation of Animals* 5, which is the most sustained discussion of the role of the environment in generation. Unfortunately the evidence that Aristotle thinks the environment plays this kind of causal role is weak. Instead he tends to treats the environment as a direct cause of features in its own right. A paradigm case is the formation of hair in wild animals:

> The condition of sheep in cold climates is opposite to that of man; the hair of the Scythians is soft but that of the Sauromatic sheep is hard. The cause (αἴτιον) of this is the same as it is in all wild animals: the cold air hardens and solidifies them by drying them; for as the heat is pressed out the moisture evaporates; and both hair and skin become earthy and hard. In wild animals, then, the exposure to the cold is the cause of hardness in the hair, while in the others it is their environment's being of such a kind. A proof of this is also what happens in the sea-urchins which

> are used as a remedy in stranguries. For these, too, though small themselves, have large and hard spines because the sea in which they live is cold on account of its depth (for they are found in sixty fathoms and even more). The spines are large because the growth of the body is diverted to them, since having little heat in them they do not concoct their nutriment and so have much residual matter and it is from this that spines, hairs, and such things are formed; they are hard and petrified owing to the congealing effect of the cold [sc. sea water]. (*GA* 5.3, 783a12-29 Platt translation with modifications)

In the case of the sea urchin, for example, the environment does not act as a trigger for the activation of a δύναμις for hard spikes. Instead the cold water itself is causally responsible for forming those parts: as the nutriment is streaming from its body during development, the cold congeals it into hard spikes. This is typical of the role Aristotle assigns to the environment in

GA 5. But this is not what the epigenesist has in mind by environmentally-induced phenotypic variation.[25]

Conclusion

At the end of her paper Leunissen (2013, 45) addresses the concern that her reading implies that Aristotle thinks formal natures deliberate and form conscious intentions in some literal way. She attempts to deflect this worry by pointing to Aristotle's cryptic remark towards the end of *Physics* 2.8 that "even art does not deliberate" (199b26-30). Now it is certainly true that *artists* deliberate and make decisions about how to act based on their

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[25] Sex determination might be seen as a counter-example to my argument, since Aristotle clearly thinks that whether or not an embryo becomes male or female is temperature dependent. (I am grateful to Maggie O'Brien for this point.) However, this is not epigenetic in the right way. Aristotle holds that "male" and "female" in the primary sense refer to the ability and inability to concoct blood into semen, respectively. And whether or not an animal acquires this dispositional property (and thus whether it becomes male or female) depends on how much the embryo is heated at conception (*GA* 4.1-2). So sex is influenced by temperature, but in a very direct way; it is a straightforward case of heating and cooling. The semen is hot and it attempts to heat the menstrual fluid to the same degree making it a male embryo. But sometimes the menstrual fluid is too cold in which case the semen fails to exercise its heating capacity sufficiently, resulting in a colder (female) embryo. There is nothing epigenetic about this account. Semen has an active power to heat the menstrual fluid, which it has in virtue of its own natural heat. And this is a standard non-rational power; it is a power for heating and only heating. If the matter is well-disposed to being heated, then the semen will exercise that power without impediment and assimilate the matter to its own hot nature resulting in a male embryo. If the matter is too cold relative to the heat in the semen, then the semen will not be able to exercise that power adequately leaving a cold (female) embryo. (See *GA* 766a19-24; cf. *GA* 4.2 and Henry 2007, 5-7.) This is no more epigenetic than saying that fire has the power to heat water and assimilate it to its own temperature but that when the water is excessively cold it fails to heat it up to the same degree. Fire does not have a power for heating *or* cooling; it has a power for heating only. And that power can be successful or unsuccessful in bringing about its effect depending on the condition of the patient and/or the external environment.

conclusions. But Leunissen argues that "the psychological states of the artist only matter in the sense that art cannot exercise itself, but operates through the artist" (Leunissen 2013, 45). But this is not quite right. It may be true that the τέχνη itself doesn't deliberate; after all, it is only a causal power. But *Metaphysics* 9.5 makes it clear that the decisions of the artist are not inconsequential. On the contrary, they are a necessary condition for the activation of that power insofar as those decisions control which of its effects comes about:

> For, while all non-rational powers are productive of a single effect only, rational powers are productive of opposites so that one power will simultaneously produce contraries. But this is impossible. Therefore, there must be some other thing that exerts control, namely, desire or decision. For whichever outcome it desires decisively, it will produce this when it is in those circumstances that are appropriate to its capacity and associates with the patient.

With rational powers (including crafts) the presence of the corresponding passive power under the right conditions is necessary *but not* sufficient to bring about the effect. There must a rational desire on the part of the agent — a προαίρεσις — that controls which of the alternative ways of activating the power will occur. So the psychological states of the craftsman do matter a great deal. It is not just that crafts must be embodied to operate; without decisions crafts would be causally inert.[26] This is why I have argued that, if Leunissen's interpretation is correct, there most certainly would be a need to attribute genuine decisions to formal natures insofar as she makes the formal nature the controlling factor that determines which of the many alternative pathways specified by the inherited potential for form get actualized during development. On my reading, since all the capacities involved in development are of the non-rational sort, there is no need for anything to make decisions about how to active them. Their activation is necessitated by contact with their corresponding powers under the right causal conditions.

In this paper I have argued that, although Aristotle clearly defended Epigenesis-1 (a thesis about the gradual emergence of form and structure), there is no good evidence that he

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[26] This strikes me as a persistent difficulty with Leunissen's work on natural teleology, namely, she never quite shows us how to get past the metaphor of nature as craftsman (see also Gotthelf and Leunissen 2012, 131-2).

endorsed Epigenesis-2 (a claim about the ability of developing embryos to adjust their phenotypes in response to novel circumstances). Moreover, I have argued that the challenge for anyone who thinks he did endorse this kind of model is to show that he had the conceptual resources to make it work without assigning embryos real-time decision-making capacities. To end this paper let me point to one further reason for thinking that the whole notion of adaptive developmental complexity, so obvious to modern embryologists, was not even on Aristotle's radar.

In *Physics* 2.8 Aristotle argues that if there were no natures (understood as goal-directed principles of change), then embryogenesis would be completely random:

> Moreover, in the case of embryos (ἐν τοῖς σπέρμασι), anything must come to be at random. But the person who asserts this does away with nature and what exists by nature entirely. For those things are natural which, by a continuous process originating from an internal principle, arrive at some end. The same end is not reached from every principle, nor any chance end, but always the tendency in each is towards the same end, if there is no impediment. (194b14-18 translated after Hardie & Gaye)

It is the last sentence that is most relevant here: developing organisms have an intrinsic disposition (or nature) to move towards a certain end state, which they will achieve *if* there are no impediments. Aristotle often makes this qualification in connection with development. And one gets the distinct impression that he thinks the absence of impediments is a necessary condition for developmental success. What we never find (and this is the key point) is any suggestion that Aristotle thinks a developing embryo has the intrinsic capabilities necessary to adjust its trajectory in order to overcome impediments. This is striking. Aristotle devotes close to five chapters in *GA* to discussing the kinds of deformities that result when impediments derail the process. And yet there is no discussion (or even recognition) of the ability of nature to recover from such perturbations and avoid those kinds of monstrosities. If Aristotle really did recognize the possibility of Epigenesis-2, then we should expect at least one chapter devoted to that. For there is no doubt that Aristotle would have championed the capacity of embryos to "stay on target" in the face of impediments as the strongest possible evidence of nature's immanent teleological character. As Peter Calow (1976, 9) puts it, in these cases it's as if the developing embryo knows exactly what it wants to be and, even in the face of violent

and unpredictable disturbances, still manages to achieve its ambition. But this is not something Aristotle seems to have noticed.

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