

REPRESENTATION IN THE GENOME

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Statement by the candidate

This thesis is wholly my original work.

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Abstract

Many biologists, and others, use representational talk to describe a range of genomic phenomena: ‘transcription’, ‘translation’, ‘error correction’, ‘the genetic code’, ‘the book of life’ etc. How seriously we should take this depends on our account of representation. ‘Teleosemantics’ is an account that bases representational content on the functions of biological systems (‘devices’) that produce and consume physical tokens so as to communicate with one another and deal successfully with the world. For example, the content of an imperative token might be thought of as the state of affairs that it is the token’s biological function to bring about.

On this view, many biological systems other than human beings display representational capacities. In particular, molecular genes within a cell, working with other cellular machinery, send messages to the ribosomes about what proteins to synthesise, how much and when. These messages are crucial to nearly all biological processes and, on a teleosemantic view, genuinely represent both the proteins that are to be synthesised and the environmental conditions with which those proteins are supposed to deal. It is tempting to think that a gene could also represent a trait — e.g. that the allele for yellow seeds in garden peas represents yellow seeds — but it does not turn out that way. The trouble is that there is no single consumer device to which the molecular gene is sending a message.

Most representation in the genome is fairly rudimentary: it is not nearly as sophisticated as, for example, a human natural language. In some cases, however, the genome displays more sophisticated capacities: biological clocks have evolved to represent future states of affairs and many viruses and bacteria practice genetic deception on host organisms.

This essay also explores two attributes that are fundamental to the genome’s representational power: the compositionality of the parts that make it up and the arbitrariness of the genetic code that underpins the expression of molecular genes.

Finally, we consider three ways of disputing the teleosemantic story about representation in the genome. First, does our story commit us to hold that representation is generated by functions underpinned by selection operating on inheritance systems other than the genome? There are many possibilities: DNA methylation, hormonal inheritance systems, environmental niche construction, symbiosis etc. This is mostly an empirical matter and, in the current state of knowledge, the answer is largely in the negative. Second, is representational talk about the genome somehow second-rate: *just* a metaphor or an analogy or a useful model? In all three cases, my answer is ‘No’. Such worries boil down to worries about the teleosemantic story itself: they do not constitute independent reasons to deny that the genome has representational

capacities. Third, does according representational status to various nucleic acid structures do genuine conceptual work? Yes, it does. It improves the coherence of our world view, presents a range of opportunities for further work, and has important implications for the way we should see humans' place in the world of representation.

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1 Introduction

To begin with a statement of the obvious, people talk to one another. They also make marks on pieces of paper, make little bumps on DVDs, inscribe spiral scratches on vinyl discs, carve grooves into lumps of stone and tie strings into knots. What causes this behaviour and what its effects are differ very much from instance to instance. The same words in different contexts have very different causes and provoke very different effects. Suppose Alcibiades and Bias encounter one another on the street and Alcibiades asks Bias ‘Excuse me. Which way is the lake?’ Bias points east and says ‘That way.’ The lake is to the west. There is no lake to the east. Alcibiades walks off to the east. In these circumstances we would have no hesitation in agreeing that Bias’s statement was false, though in reaching this conclusion, a number of features of the context are relevant:

- o A and B are not on stage performing a play or in some other ‘pretend’ situation;
- o they are strangers, so they are not using in-jokes or idiolects;
- o A’s polite ‘Excuse me’ functions as a signal that the following question is a genuine request for information rather than a joke (‘Where’s the fire?’) or a challenge (‘What are you looking at?’);
- o they are on a street so the choice of which direction to take is binary — there’s no chance of misunderstanding a pointing eastwards with a direction to go west; and
- o a lake is a nice big thing that is reasonably easy for a human to recognise, and there’s only one of them in the vicinity, so B is not likely to misunderstand what A wants to know.

There are probably other things we would need to know before we could be sure that A is genuinely seeking information and that B understands this but the point is clear enough: speakers and hearers habitually communicate by means of the representational tokens of natural languages and, at least sometimes, hearing these tokens allows the hearer to act in ways that promote their welfare (or that of the speaker).

But what gives the token its meaning? It is no easy matter to give an account that can explain:

- o the fine distinctions of meaning that we use every day, often without conscious consideration;

- o how we can sometimes use language to convey factual information, but sometimes also to lie or mislead, to direct the actions of others or to speculate about how the world might have been or could be. These uses seem to be representational but not factual;
- o how our statements of fact can sometimes be false and our directions not complied with;
- o how the behavioural consequences of consuming representational tokens can be so widely separated in time from the initial consumption; and
- o how we can speak about people we have never met, or places we have never been, or about events that have never happened, and will never happen.

An obvious move is to say that an utterance, or some other public representational token, expresses a thought harboured by the speaker. Bias pointed east and says ‘That way’ but he could have expressed the same meaning by pointing and saying ‘Down there’ or by saying ‘To the east’ or ‘In the direction of the rising sun’. This does not, however, advance us very far. The same puzzling features of utterances also arise in relation to the thoughts they express.

1.1 An evolutionary perspective

One approach to the question is to see linguistic tokens — sentences, words, morphemes and phonemes — and the more mysterious mental representation tokens that underlie them, as biological phenomena, the product of sub-organismal systems that have evolved because of the contribution that they make to the survival and reproduction of the organisms that contain those systems.

If we can make such a theory work, we may be able to understand how representational systems come to be by understanding how they have been built incrementally, and to understand the most sophisticated representational systems as elaborate versions of much simpler systems.

Starting from this evolutionary perspective, Millikan, Papineau and others have offered a ‘teleosemantic’ account of linguistic and mental representation under which, broadly speaking:

- o the content of a representational token is determined by reference (one way or another) to the biological function of the systems that produce and consume it; and
- o a biological function of a system at a point in time is something (though perhaps not *any* thing) that the system and its ancestors have done that helps to account, in evolutionary terms, for the existence of the system at that point.

Whichever account of function we choose, though, a teleosemantic account of representational content in natural language seems almost inevitably to raise the question whether other biological systems — either organisms or sub-organismal systems — can do the same.

1.1.1 Animal signaling

It is tolerably clear that organisms of other species communicate with one another by the use of signs. Vervet monkeys are preyed upon by a number of small carnivores, leopards, eagles, baboons and pythons. Vervets give different alarm calls to warn one another that a predator is in the offing. Each call evokes a different response from the vervets that hear it. ‘Leopard’ calls cause hearer vervets to run into trees, ‘eagle’ calls cause them to look into the air and so on (Cheney and Seyfarth 1985). It is less clear whether the tokens produced by vervets possess representational content in the same way as human natural languages do. There are some fundamental differences, particularly that:

- o vervet calls have none of the compositionality that marks human natural languages. Each call is given separately. Calls are not combined into larger units whose significance varies according to the calls that are combined and the way they are combined;
- o the link between the circumstances that usually prompt the making of a particular kind of call and the call itself is inflexible. So far as we know, vervet calls are not under the sort of top-down control that might allow them to be repressed in circumstances where the usual response would do more harm than good;
- o on the other side of the transaction, vervet calls are closely linked to particular responses on the part of hearers. In Sterelny’s terms, they are intimately ‘coupled’ to particular responses. A vervet that hears a ‘leopard’ call runs up a tree. It does not combine the incoming call with other representations and respond in any one of a number of ways, or fail to respond at all.

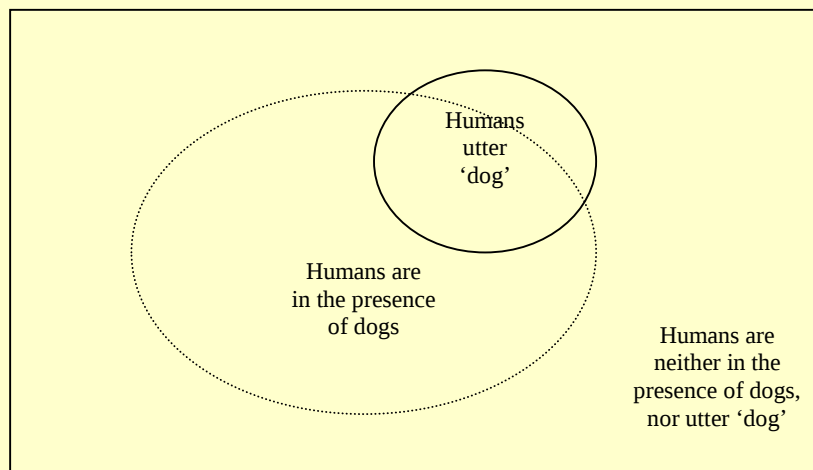
Still, there seem to be at least some important similarities.

- o The calls of one vervet effectively coordinate the behaviour of other vervets in ways that usually benefit them.
- o The perceptual and cognitive systems that collaborate to produce such tokens — setting aside for the moment the question whether tokens produced by non-human animals possess genuine representational content — are the products of evolution and, it seems

beyond doubt, have been selected, at least in part, for their capacity to produce such tokens.

- o Particular vervet calls reliably covary with particular types of states of affairs in the outside world. Of course, the relationships between the utterances of particular sentences in natural languages do not covary with states of affairs in the outside world in any very simple way. Utterances of the word 'dog' are probably more frequent in situations where dogs are present than in situations where they are not, but it may well not be the case that most utterances of 'dog' occur when dogs are present. The counts in a particular spatiotemporal region might look a bit like Figure 1.¹ Still, there is some correlation between having dogs around and using 'dog'. In particular, it seems fair to surmise that there is also a correlation between talking about dogs and doing something in relation to a dog and that people are more likely to talk about dogs when they are about to do something to or with a dog than they are when a dog is merely in the vicinity.

Figure 1: Dogs and utterances of 'dog'



¹ This would read something like, 'In Tasmania in 1899: (a) of all human life-minutes, 35 per cent were spent in the presence of dogs and 65 per cent not in the presence of dogs; and (b) of all utterances of 'dog', 73 per cent occurred while the utterer was in the presence of a dog and 27 while the utterer was not in the presence of a dog.'

All of this is no more than suggestive, but we know that humans, who are evolved animals, definitely produce tokens with representational content that are sometimes consumed by other humans. And it looks very much as though other evolved animals like the vervets do likewise.²

1.1.2 Sub-organismal systems: hormones

So the question suggests itself, whether such tokens are produced and consumed only by individual organisms or whether there are also sub-organismal biological systems that produce and consume representational tokens?

A full answer will have to wait until we have a clearer view of what constitutes representation, but at this point we can at least observe that coordination problems, addressed through signaling systems arise often at a sub-organismal level. Different anatomical systems have to coordinate their activities in order to maintain stable conditions within the organism. While the overlap of interests between different sub-organismal systems may not in all cases be perfect (Haig 1993; Burt and Trivers 1998), we can expect that in most cases the degree of overlap will be considerable.

Complex hormonal systems are a good example of systems that have evolved to solve coordination problems in multicellular organisms. Warm-blooded ('homeothermic') animals maintain a more or less constant body temperature. To do this, an animal must produce more heat in colder environments. When the ambient temperature falls below a certain point, the body uses a number of mechanisms to produce more heat ('adaptive thermogenesis'). Curling into a ball and shivering are short term solutions but if cold conditions persist, other mechanisms are triggered.

In particular, the production of more heat is primarily regulated by thyroid hormone (Silva 2006). When it gets cold and stays cold, thyroid hormone directly controls critical steps in the production of body heat. It increases fuel availability by increasing appetite and stimulating fat production in the liver and it increases the delivery of oxygen and fuel to tissues by stimulating cardiovascular function and fat breakdown in the tissues.

As one might expect, the systems in which hormones take part are very complicated. In the case of thermogenesis, thyroid hormone works with the sympathetic nervous system practically at all

² We will return to animal signaling when we come to consider the conceptual significance of attributing representational capacities to nucleic acid structures, in section 9.

levels. The interaction is most evident in a type of body fat, brown adipose tissue, where additional heat cannot be created without activity of the sympathetic nervous system but where the responsiveness of the tissue is dependent on high concentrations of the most active form of thyroid hormone.

There are many other examples of hormones acting as the regulators of biological processes that are geared to environmental conditions (both within and outside the organism).

- o Physical stressors — such as trauma, infection, intense heat or cold, and allergic reactions — induce the adrenal glands to make more hydrocortisone, which accelerates the metabolism of carbohydrates. If the adrenal glands do not respond, this can be a life-threatening problem.
- o If a person has too little calcium in their diet, the parathyroid glands produce and excrete parathyroid hormone, which works to transfer calcium from the bones to the blood so that it will be available for nerve conduction and muscle contraction.
- o A number of lipids (roughly, fat molecules) also trigger cellular processes in response to conditions within and outside the cell.³ For example, sphingosine-1-phosphate, is a potent ‘messenger molecule’ involved in regulating calcium mobilization, cell growth, cell death (‘apoptosis’) and, interestingly, DNA acetylation (Spiegel and Milstein 2003).

I am not arguing at this point that hormone synthesis, or other features of the endocrine system, bear representational content. I am only suggesting that:

- o the internal environment of organisms poses coordination and decision problems strikingly similar to those posed by the external environment; and
- o the fact that the systems that deal with these problems look like they involve messengers carrying information around the body is a good motivation to ask the question whether basic biological systems could possess representational content.

³ I add scare quotes so as not to prejudge whether genuine representation is going on here.

The situation of sub-organismal systems fits very naturally into the kind of signaling models explored by Lewis (2002) and Skyrms (2010). These models, in their simpler forms, involve:

- o a producer system that can detect a state of affairs in the environment and can transmit a signal to other systems, but cannot act itself to deal with the states of affairs that it detects; and
- o a consumer system that can register signals and respond to them, but cannot itself detect states of affairs in its environment.

The parallel with the relationship between an organism's sensory and motor systems is clear enough.

1.2 Representational content in the genes?

Hormones are synthesized within living cells — under particular circumstances — by reference to a template in the cell's DNA. That is, the amino acids that constitute a hormone are assembled in a pattern determined by the arrangement of nucleotides in the organism's DNA (although whether the hormone is synthesised and how much of it is synthesised depends on complex interactions within the cell). So, since:

- o we can find a variety of sub-organismal systems that appear to send signals to one another, in response to conditions in the environment;
- o the function of the chemical signals — often hormones — is to elicit from the consumer device a response that will help the organism of which the systems are a part survive and reproduce; and
- o the chemical signals are themselves synthesized from molecular genes in the organism's DNA;

it seems reasonable to ask whether the molecular genes — the stretches of DNA — that function as templates for the synthesis of hormones, other signaling molecules and a vast range of other proteins, also bear representational content. The question seems particularly natural in light of the complex regulatory systems that match molecular gene expression with external states of affairs or with other processes at work within the organism. Molecular genes do not just churn out their products willy-nilly; their contribution to the survival and reproduction of the systems of which they form a part depends on their being turned on and off at the right time, and to the right extent.

The control of gene expression depends on the solution to communication and coordination problems both within the organism and between the organism and its environment.

Molecular genes, and other nucleic acid structures like RNAs, are composed of long strings of nucleotides of only four kinds (see section 2), and are found repeated in every cell of the organism (with the exception of the red blood cells). Their order influences (to a considerable extent, at least) an enormous range of phenotypic traits, including, in humans, eye colour, intelligence, height, skin colour and a host of rare physical conditions. Moreover, many biologists attribute a special role to molecular genes in both development and evolution.

- o At the extreme, some people regard molecular genes as a complete set of instructions for the development of an organism — so that other resources necessary for development are relegated to a secondary enabling status, while molecular genes are the only factors that make a genuine difference in the morphology of a particular organism.
- o In relation to evolution, it is often held that molecular genes are the only biological entities that are directly copied from generation to generation of any lineage: they are the replicators upon which natural selection operates. In this way too, molecular genes are special.

As it turns out, I think that both theses positions are too strong (see section 7) but even if we do not want to go this far, it remains the case that molecular genes — with their causal potency, their central role in ontogenesis and evolution, and their linear compositionality — certainly look as though they might bear representational content in the same kind of way as the tokens of natural languages do.⁴

Moreover, talk of information contained in and conveyed by the genome is pervasive in evolutionary biology (Nijhout 1990):

The collection of chromosomes in the fertilised egg constitutes the complete set of instructions for development, determining the timing and details of the formation of the heart, the central nervous system, the immune system, and every other organ and tissue required for life. (DeLisi 1988, p.488)

⁴ Molecular genes are not the only sub-personal systems that could bear representational content. Modules in the brain, if there are any, might also act as producers and consumers of representations, as might non-neural structures and processes like glands secreting hormones.

In later organisms the content of common information conserved is so high that humans share nearly 40 per cent of their information with plants and nearly 99 per cent with chimpanzees ... (Goonatilake 1991, p.121)

This [natural selection] involves two essential processes: (1) the occurrence of random *variation* in the genetic information passed from an individual to its descendants and (2) *selection* in favor of genetic information that helps its possessors to survive and propagate. (Alberts, Bray et al. 1994)

The information required to make a complete organism is contained within the genes of the genome. (Burglin 2006, p.34)

1.3 Natural information and representational content

What does this talk of information mean? It is common ground in the literature, that we can distinguish two quite different kinds of information. ‘Natural information’ (Grice 1989, p.214) is information conveyed when the state of one system, the sender, can be inferred — with greater or less certainty — from the state of another system, the receiver, because the state of the receiver reliably covaries with the state of the sender. It is also sometimes referred to as ‘Shannon information’ (Shannon 1949), ‘correlational information’ or ‘causal information’.

Suppose we cut down a living tree and find that the tree ring third in from the outside is particularly narrow. The narrow tree ring conveys the natural information that the year before last was colder than usual because cold weather causes trees to grow slowly and warm weather causes them to grow quickly. The state of the receiver, the tree rings, is causally linked through a channel, the tree over time, to the state of the sender, the weather in the vicinity of the tree over time. If the channel is noiseless, the state of the receiver is a function only of the state of the sender. In practice, nearly all channels have some element of noise, i.e. the state of the receiver is causally influenced by factors uncorrelated with the state of the sender. The year before last may not have been cold; something else may have caused the tree’s slow growth — a fungus or a chemical spill.

There will often be a direct causal link between sender system and the receiver system but this is not necessary for the receiver to bear natural information about the sender. Suppose particular changes in the state of a system A cause particular changes in the state of systems B and C but that there is no causal link between B and C. In this case the state of B bears natural information about the state of C even though there is no causal link between the two (Dretske 1981, p.36).

In some cases information talk in evolutionary biology or molecular genetics can be construed in this reasonably simple, covariation-based sense but, as Griffiths points out (2001, p.394), such talk is often used in contexts where it clearly refers to a richer concept of information, in particular what is often called ‘semantic information’ — or ‘non-natural information’ (Grice 1957, p.378) or ‘intentional information’. Such information:

- o is about something. A path of broken vegetation running down a hillside conveys (imperfect) natural information about a rolling boulder (if there’s the first, the second has been there) but we do not say that the path is about a boulder or that it refers to a boulder as we do say that the words ‘Queen Elizabeth the Second’, in normal usage, are about, and refer to, the British monarch;
- o can be right or wrong. Paths of broken vegetation running down hillsides covary imperfectly with rolling boulders. But if we find a path created in some other way, we do not say that the path is false (whether or not anyone has inferred the passage of a boulder from it), as we do say that the statement ‘Queen Elizabeth the Second weighs more than a tonne’ is false (whether or not anyone believes it);
 - We might well say that the path is false if it has been deliberately left by a human to mislead the observer. In this case, it would bear (false, indicative) content. In section 5.2 I will provide a more detailed account of deception, in the genome and elsewhere.
- o can be imperative or normative as well as indicative or descriptive (Godfrey-Smith and Sterelny 2006). Paths of broken vegetation bear natural information about rolling boulders but they cannot tell a boulder to roll or prohibit one from doing so, as we can and do use language to issue commands or prohibitions: ‘Bow when you meet Queen Elizabeth the Second.’

I’ll generally avoid talk of ‘semantic information’ and talk instead of ‘representational content’. But I mean the two to be synonymous: some entity or system or process bears semantic information if and only if it bears representational content and the semantic information harboured is identical with the representational content.

1.4 Structure of this essay

Natural languages are the paradigm examples of a system that bears representational content and the parallels between nucleotides and letters, between codons and words, between amino acids

and the referents of words seem obvious enough (see section 4.1). That molecular biologists have adopted linguistic terminology to describe the processes by which cells and organisms are built and reproduced seems to me an entirely natural use of metaphor, rather than the somewhat sinister marketing device as which it is sometimes portrayed (Keller 1995, p.18).

But is there anything more to these linguistic metaphors than metaphor? Some of the quotes set out above certainly seem flatfootedly literal. So my aims in this essay are to determine whether DNA or other nucleic acid structures bear representational content (on a particular, teleosemantic, view about what constitutes such content) and, if so, to identify what that content might be.

I will also argue that seeing DNA and other nucleic acid structures as bearing representational content provides us with explanatory and predictive purchase on these phenomena and others with which they are associated.

Section 2 sets out some biological background.

Section 3 canvasses a number of teleosemantic theories of representation. I settle on Millikan's version as the most plausible, but we will bear other theories in mind, particularly Shea's, as we explore the application of teleosemantic theories of representation to the genome.

Section 4 will consider three kinds of genetic structure which one might think bear representational content.

- o First, and most immediately, one might think that molecular genes, i.e. coding regions of DNA, represent the polypeptides for whose synthesis they act as a template.
 - I conclude that on Millikan's account, though not on Shea's, this is indeed the case.
- o Second, one might think that some collections of molecular genes, particularly those that influence the body plan of the organism in development represent not just the polypeptides for whose synthesis they act as a template but the phenotypic traits in which they are causally implicated.
 - Despite the intuitive attractions of this idea, I conclude that — under the producer-token-consumer model of representation that is under consideration in this essay — nucleic acid structures do not represent phenotypic traits, even those to whose development they make important causal contributions.

- o Third, one might think that the expression of a particular molecular gene represents the environmental conditions with which the expression of the gene helps the organism deal.
 - This I think is right: the fit with the teleosemantic model of representation is very tight.

In section 5, we look in some detail at two classes of cases in which the genome displays more sophisticated representational capacities.

- o Genetic clocks have evolved to represent future events.
- o A range of viruses and bacteria practice deception by sending messages to host cells that hijack their genetic machinery for the benefit of the virus or bacterium.

In section 6, we explore two related but distinct attributes of the genome that are fundamental to its representational power: the compositionality of the parts that make up the genome and the arbitrariness of the genetic code that underpins the expression of molecular genes.

Having set out this teleosemantic account of representation in the genome, we will discuss three challenges to such a story.

First, we will consider whether a teleosemantic account of representation commits us to recognising too much representation in the world around us: if molecular genes, or other nucleic acid structures, bear representational content, are we obliged to attribute representational properties to a range of biological phenomena we do not want to see as representational?

- o My conclusion is that, as a matter of biological fact, we are rarely if ever obliged to accept this kind of unwelcome conclusion.

Second, we will consider a family of claims that talk of representational content in the genome is, in some way, less than serious:

- o that such talk is metaphorical or analogical in some epistemically second rate sense; or
- o that representational systems can function as a useful model of various genomic phenomena but that we should not ascribe full-fledged representational content to such phenomena.

- In all these cases I argue that such claims boil down to worries of one kind or another about the teleosemantic account of representation. They do not constitute *independent* considerations that tell against that account.

Third, we will consider whether according representational status to various nucleic acid structures does genuine explanatory work in genetics or biology more generally. Even if we can ascribe representational content to some nucleic acid structures without absurdity, how does this help us to understand biology, evolution or genetics? In other words, so what?

- o I argue that a representational account of some nucleic acid structures improves the coherence of our world view, presents a range of opportunities for further work, and has important implications for the way we should see humans' place in the world of representation.

Finally, the conclusions I have just outlined will be drawn together to give what I hope is a coherent and convincing account of representation in the genome.

2 Biological background

2.1 Cells, macromolecules and life on earth

With the exception of viruses, which we will set to one side for the moment, all living things are made up of cells. All cells are made up of four kinds of macromolecule — proteins, nucleic acids, lipids and carbohydrates — as well as smaller molecules. It is the macromolecules that participate in cell metabolism and cell structure.

Proteins can function as:

- o structural components within an organism that make up, for example, hair or the skeleton of a cell — tubulin and collagen are examples;
- o enzymes, that is, catalysts of chemical reactions that may, for example, digest food, generate energy or synthesise signal molecules in neurons;
- o antibodies that inactivate bacteria or viruses; or
- o conveyers of molecules, for example haemoglobin, which transports oxygen through the body.

Nucleic acids of many kinds play a central role in the synthesis and transformation (‘metabolism’) of macromolecules. Either DNA or RNA molecules are found in every cell of every organism. A DNA molecule is a pair of long strands of components known as nucleotides, each of which consists of a phosphate group, a deoxyribose sugar molecule, and one of four different nitrogenous bases, adenine, guanine, cytosine, or thymine. There are four kinds of nucleotides that appear along the strands of DNA: cytosine (C), guanine (G), adenine (A) and thymine (T). Each is consistently paired with another kind of nucleotide on the other strand: C with G, G with C, A with T and T with A.

DNA is causally central to the synthesis of the proteins that go to build new cells, and thus to the development of the individual organism, and to the reproduction of the organism in the next generation (see below).

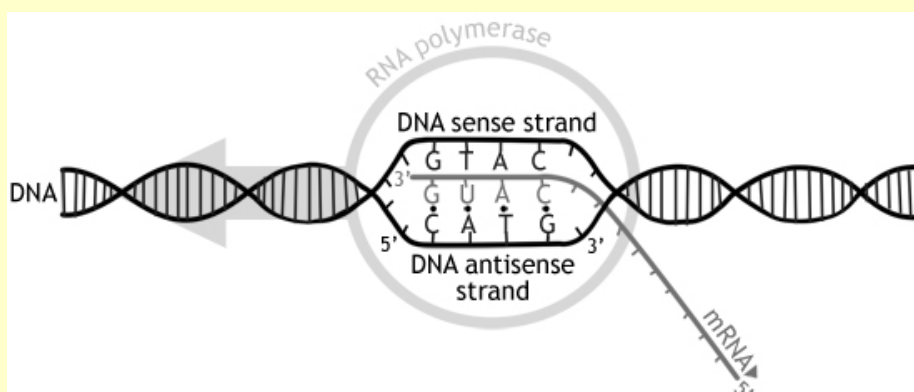
The cells of all organisms are either prokaryotic or eukaryotic. Prokaryotic cells have no cell nucleus, or indeed any other membrane-bound cell structures (‘organelles’). Nearly all prokaryotic organisms are unicellular. They include bacteria and archaea.

Eukaryotic cells are more complex. The genetic material — DNA and a variety of other proteins — is contained in a membrane-bound nucleus. Eukaryotic organisms include animals, plants, and fungi — which are mostly multicellular — as well as single celled organisms ('protists').

2.2 Protein synthesis

A protein-coding region is activated when a 'transcription factor' attaches to the DNA in a regulatory region of the genome. Each transcription factor has a particular short DNA sequence, a 'binding site' to which it attaches. The transcription factors attached in the regulatory region make the protein-coding region accessible so that the enzyme RNA polymerase can transcribe the DNA into precursor RNA. The precursor RNA is then spliced to remove introns, which do not code for proteins, leaving only the exons, which do. The spliced precursor RNA is known as messenger RNA (mRNA). This process, in which a stretch of mRNA is derived from a protein-coding region of DNA is known as transcription (Burglin 2006, p.19). Although only one DNA strand is transcribed in any particular region, both strands of DNA may be transcribed in adjacent regions (see Figure 2).

Figure 2: Transcription



Source: commons.wikimedia.org

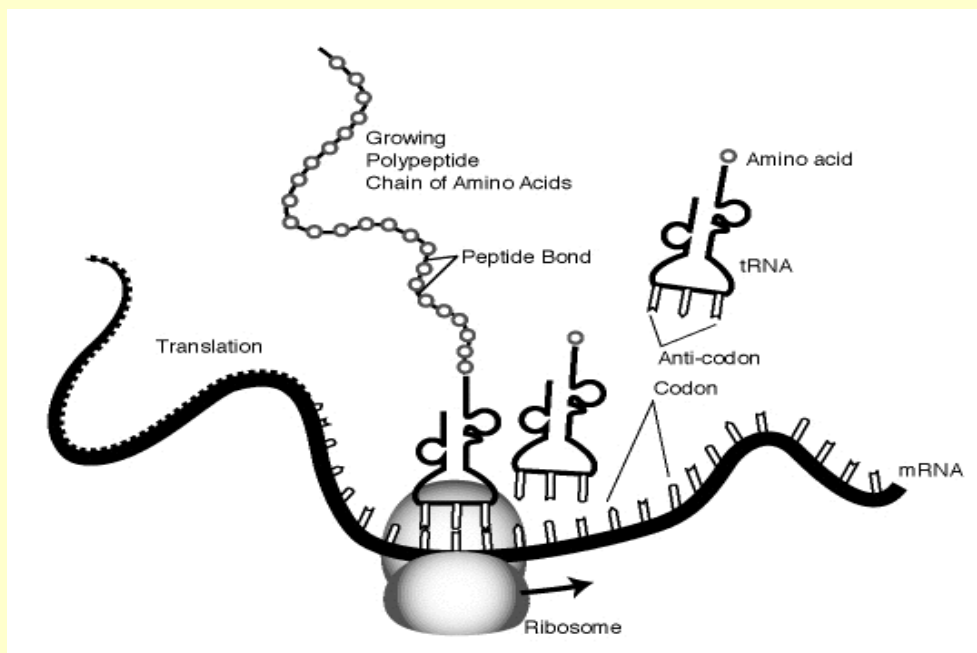
The mRNA transcript molecule represents a 'working copy' of the strand of DNA. Like DNA, it is composed of nucleotides, but its nucleotides contain the sugar ribose rather than deoxyribose. Furthermore, instead of thymine, RNA contains uracil, a base that has hydrogen-bonding properties identical with those of thymine.

The process by which a protein is derived from a protein-coding region of mRNA is known as 'translation' and begins when the ribosome, outside the cell nucleus, binds to the start codon in the protein-coding region in the mRNA.

The ribosome is a subcellular particle, found in large numbers in all cells, either floating free in the cytoplasm, or attached to the cell wall. Bacteria contain approximately 10,000 ribosomes, and eukaryotic cells over 50,000.

At the ribosome another kind of RNA molecule, tRNA, binds to specific three-base sequences of mRNA ('codons'). A tRNA molecule consists of a single nucleotide triplet bound to a single amino acid so that, via tRNA, each codon in the mRNA is associated with a particular amino acid. There are between one and four known tRNAs for each amino acid (Gardner and Snustad 1984, 248). As the ribosome moves along the mRNA sequence, through trial and error, it locates a tRNA molecule that corresponds to the current triplet in the mRNA and assembles the amino acids from the tRNA molecules into a protein (see Figure 3).

Figure 3: Translation



Source: National Institutes of Health (public domain)

It is important to be clear that, in many cases there is no very straightforward relationship between a linear sequence of bases along the dual strands of DNA and the protein (or proteins) for whose synthesis that sequence acts as a template.

So any claims that we make about a nucleic acid structure representing:

- o a particular protein (most obviously, the peptide for whose synthesis it can sometimes act as a template); or

- o a particular state of affairs in the environment (perhaps the state of affairs in response to which protein synthesis is initiated); or
- o a particular phenotype (one to which, for example, the nucleic acid structure makes an important contribution);

will need to respect the indirect nature of the DNA-to-protein relationship.

2.2.1 Reading frames

DNA has a directional structure. One end has the fifth carbon in a deoxyribose molecule at its terminus; the other end terminates in the third carbon of the final nucleotide (Hartwell, Hood et al. 2000, p.150) So any sequence of nucleotides on a strand of RNA can be translated into a string of amino acids in six ways, depending on:

- o the direction in which the sequence is 'read' – from the 5' or the 3' end of the strand; and
- o which nucleotide is taken as the first of the sequence to be translated.

Where the translation of the mRNA begins depends on the occurrence of the start codon, AUG. When the mRNA reaches the ribosome, which 'reads' it base by base, translation only begins when the ribosome reaches an AUG codon.

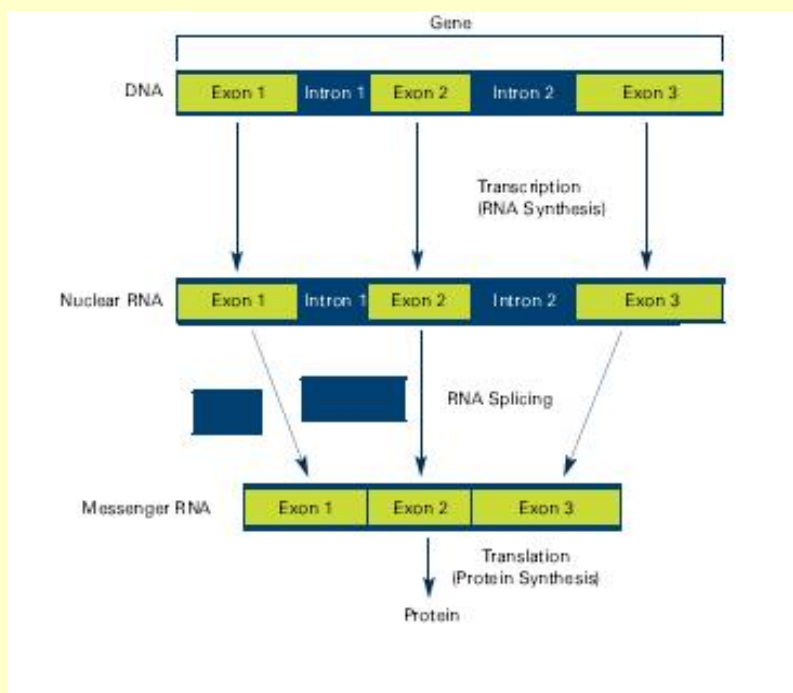
2.2.2 RNA processing

In prokaryotic organisms, the 'primary transcript' generated from the DNA template by RNA polymerase is the molecule that guides the assembly of amino acids into a protein. But in eukaryotes, most primary transcripts are subject to a considerable amount of processing in the nucleus before they migrate to the ribosome and participate in translation there. There are two types of processing: capping the ends of the primary transcript; and removing a number of nucleotide sequences from it (Hartwell, Hood et al. 2000, p.233).

- o *Capping.* In eukaryotes, the nucleotide at the 5' end of a processed mRNA is a guanine in reverse orientation from the rest of the molecule and connected through a triphosphate linkage with the first nucleotide in the primary transcript. The guanine is not transcribed from the DNA but added by a specialised capping enzyme. Another group of enzymes ('methyl transferases') then add methyl groups to the reversed guanine and to one or more of the following nucleotides forming a 'methylated cap'. The cap does not specify an amino acid in the completed protein, but is critical for efficient translation.

- o *Removing sequences from the primary transcript.* The primary mRNA transcript contains bases corresponding to every base in the parent DNA. A number of regions ('introns') are then removed from the primary transcript and the remaining regions ('exons') are then spliced together, usually (though not always) in the same order in which they appeared in the original DNA (see Figure 4). Three types of short sequence in the primary transcript 'splice donors', 'splice acceptors' and 'branch sites' dictate the splicing sites. The spliceosome is a structure within the nucleus that catalyses splicing. It is comprised of five small nuclear RNAs ('snRNAs'), four small nuclear ribonucleic particles ('snNRPs') and around 50 specific protein molecules. Not all eukaryotic molecular genes contain introns, though the large majority do. Most human genes contain introns, between 1 and 60. In some cases the introns are, in aggregate, much longer than the exons. For example, the DNA of the dystrophin molecular gene in human beings and the primary mRNA transcript derived from it both have 2.5 million bases while the processed mRNA has only 14,000. In rare cases, an intron involved in the processing of the mature mRNA for the synthesis of one protein can itself function as the entire coding sequence for the synthesis of another, unrelated protein (Stotz 2006, p.908).

Figure 4: Exons and introns



Source: *The New Genetics*, National Institutes of Health, Publication No.10, Revised April 2010, <http://www.nigms.nih.gov>

2.2.3 Alternative splicing

In some cases, the exons can be spliced together in number of different orders, to form different mature RNAs, each of which acts as a template for a different protein. Various studies estimate that between 40 and 60 per cent of human primary RNAs are alternatively spliced (Redei, Koncz et al. 2006, p.68).

- o For example, the antibodies in the immune system are composed of heavy and light chains. In mammals, alternative splicing of the primary RNA that acts as a template for the synthesis of the heavy chain determines whether the antibody proteins are embedded in the membrane of the cell that makes them (a 'B lymphocyte' in this case), or are secreted into the blood (Hartwell, Hood et al. 2000, p.237).
- o In the mitochondria of trypanosomes, a type of parasitic protozoa, U nucleotides are inserted into, and occasionally removed from, an RNA transcript. In some regions more than half the bases in the mature mRNA are Us inserted during editing. Editing also occurs in the mitochondria of many plants, where up to 10 per cent of C bases are changed to U bases, without insertions or deletions.
- o Editing also occurs in animals, though to a much more limited extent. In the *apolipoprotein-B* gene, editing produces two types of transcript, depending on the tissue in which translation occurs. In one of these a single C in the primary mRNA is changed to a U, creating a translation termination codon that causes truncation of the protein derived from the unedited transcript (Alberts, Bray et al. 1994, p.460).

2.2.4 Operons

In many prokaryotes (but not in eukaryotes) the DNA sequence that acts as a template for the synthesis of a protein performs its function only as part of a larger system. For example, in prokaryotes, a number of coding regions that act as templates for a set of proteins that function together are often found in a single continuous sequence in the DNA (Lodish, Berk et al. 2008, p.122). For example, the coding regions for the set of enzymes necessary to synthesise tryptophan are most often found in a single sequence.

Such an arrangement of coding sequences is called an 'operon', since it functions as a unit from a single promoter. Transcription of an operon results in the 'coordinate expression' of all the molecular genes in the operon.

In the case of operons, then, there is no independent correspondence between a simple molecular gene and a polypeptide but between a set of simple molecular genes and a set of polypeptides.

2.2.5 Variety in translation

Errors that alter the reading frame occur extremely rarely during translation, yet some molecular genes have evolved sequences that induce frameshifting. These ‘programmed frameshift sites’ alter the usual translation of mature mRNA into amino acids. Most frameshifts shift the reading frame one nucleotide upstream. Such sites are dispersed quite widely among evolutionarily diverse species. Downstream frameshifts are much less common, but again dispersed widely among different species. The rarest form are ‘translational hop sites’ which cause the ribosome to bypass a region of several dozen nucleotides (Farabaugh 1996).

2.2.6 Gene regulation

When a particular protein is synthesised and how much of it is synthesised depend on complex regulatory machinery within the genome, which responds to environment conditions within the cell.

So, for example, complex molecular genes, such as the *eyeless* gene in mice, do not carry instructions for a particular trait; they set in motion the expression of many other molecular genes that, together with other developmental resources, generate a particular phenotype. If the mouse *eyeless* gene is transplanted to *D. melanogaster* and activated, the phenotypic outcome is a fruitfly eye, not a mouse eye.

Moreover, a ‘transcription unit’ is not entirely composed of coding sequences. It also includes: intervening, non-coding sequences; any 5’ or 3’ trailer sequences that surround the ends of the coding sequences; and regulatory sequences included in the transcription unit. Also necessary for the generation of a functional product are regulatory sequences flanking the transcription unit (Singer and Berg 1991, 440). All this complex regulatory machinery only arises in eukaryotes. The process in prokaryotes is much simpler.

A DNA sequence that functions as a promoter region (a sequence to which RNA polymerase binds at the beginning of transcription) at one point can function as a coding sequence elsewhere (Neumann-Held 2001, 72).

2.3 Terminology

Here, without prejudice to the questions under discussion, ‘genetic code’ will be used in a relatively narrow sense to denote the mapping from codons to amino acids or to the termination of translation. Also, so as not to pre-empt questions about the role of information in the genome’s contribution to ontogeny, I shall refer to DNA’s part in the transcription-translation process, outlined above, as ‘acting as a template’ for the production of amino acids or of proteins.

‘Representational system’ will be used to mean any system that produces physical tokens that bear representational content. On a teleosemantic view, the elements of such a system will have particular kinds of biological function (see section 3 below).

Given the different senses in which ‘gene’ is used, I will try to avoid the word so far as possible. Where this is not possible, I will try to distinguish between:

- o ‘instrumental genes’ — genes conceived of as causal factors, characterised functionally rather than in terms of their physical make up, in the transmission of a heritable phenotype, or in a model of the changing phenotypic characteristics of a population over time; and
- o ‘molecular genes’ — either:
 - ‘simple molecular genes’ — genes conceived of as sequences of unambiguously transcribed codons in an organism’s DNA, e.g. *eyeless* or *sonic hedgehog*; or
 - ‘complex molecular genes’ — genes conceived of as collections of DNA structures that play the role of the instrumental gene but are not simple molecular genes, because their structural elements may not be part of the same sequence of codons and may be transcribed in different ways and produce different products.

This is essentially the useful taxonomy suggested by Griffiths and Stotz (2006) except that I use ‘simple molecular genes’ where they use ‘molecular genes’ and ‘complex molecular genes’ where they use ‘postgenomic molecular genes’, partly because the contrast between simple and complex seems to capture the fundamental distinction between the two categories (which are both assemblages of molecules) and partly just because ‘postgenomic molecular genes’ seems rather clumsy.

‘Nucleic acid structure’ will be used generically to mean any DNA or RNA structure.

3 The teleosemantic framework

One strategy for distinguishing between natural information and representational content is to adopt a ‘teleosemantic’ account of representation which holds, roughly speaking, that whether X represents something else and what that something else is, depends on the function of X (or the function of something related to X). So, for example, you might claim that when a vervet monkey emits a leopard call, the call means there’s a leopard approaching because the function of the call is to alert other vervets to the approach of a leopard.

This seems a particularly appealing choice of theory to frame an account of representation in the genome not only because it is a reasonably promising and popular view of paradigm cases of representation but also because it obviously does not prejudge the question whether sub-organismal systems have or respond to representational content.

Most such accounts in the literature rely on a conception of function that links function to evolutionary history. While I shall follow this pathway myself, I argue (section 3.1) that this is not a forced choice: one could explain content in terms of function without explaining function in terms of history.

There are many possible ways of trying to make the teleosemantic intuition more precise. What X is varies from theory to theory. It could be thought of as:

- o some physical token — like a set of sound waves or writing on a page; or
- o the process of producing the token — the act of speaking or writing;
- o the response to the token of some consuming system — the reception of the sound waves or the writing by a hearer of some kind.

‘What X (or something related to X) is supposed to do’ also varies from theory to theory but it is common ground that it should be construed in terms of *function* — so that X is supposed to do Z if it is X ’s function to do Z .

In this section, we will first consider the notion of function that underpins teleosemantic theories of representation. In line with most of the literature, we will adopt an aetiological account under which, broadly speaking, the function of an X is something that that X (or previous X s) has (have) done that explains why this X is around. We will adopt Godfrey-Smith’s ‘modern history’ account of function as suitable for the kind of genomic examples that we will be exploring in later sections.

We will then consider the different functional structures that have been proposed as ways of characterising representation. That is, we will consider what kind of entities you have to have and what functions they have to have, in order for representation to arise.

The most simple functional structures seem inadequate to capture the notion of representation. So, for example, we will have to go beyond the idea that representation arises whenever it is the function of a device to covary with some state of affairs.

I will argue that Papineau's account of representation, which finds representation in the relationship between the functions of desires and the functions of the beliefs with which the desires interact does not seem quite to distinguish representational from non-representational functions.

We will also consider Jablonka's consumer-focused story, which attributes content to the reception by a consumer device of any external phenomenon, provided that the reception contributes to the survival and reproduction of the consumer. This seems too permissive to work as an account of representation.

In the end we will settle on a relatively demanding Millikan-style account of representation, which relies on both a consumer and a producer device possessing 'adapted functions' that work together to adapt the behaviour of the consumer device to some particular state of affairs.

Finally, we will note a number of challenges to such an account, which I believe can be met, but we will not undertake a comprehensive discussion of the pros and cons.

3.1 Biological function

The notion of function is clearly problematic in itself and there is an extensive literature which tries to come up with a convincing account of the concept couched in terms of more fundamental, 'naturalistic' concepts. A full review of the issue would be a book in itself and would clearly be beyond the scope of this essay.

Since we are concerned with representation in the genome, we are primarily interested in biological function — the function of the characteristics and behaviour of living things: beaks, livers, beaver tail slaps, words spoken by humans, bee dances, bird song, hippo grunts and so on.

3.1.1 The aetiological approach to function

Most teleosemantic theories adopt an ‘aetiological’ account of biological function, and function more broadly. The first explicit account was presented by Wright (1973). Broadly speaking, such accounts take the function of *X* to be that particular consequence of its being where (or as) it is which explains why it is there (or is as it is). In more formal terms:

The function of *X* is *Z* iff:

- (1) *X* is there because it does *Z*; and
- (2) *Z* is a consequence (or result) of *X*’s being there (Wright 1973, p.161).⁵

So, for example, the heart’s function is to pump blood because:

- o the heart is there because it pumps blood; and
- o that blood is pumped around the body is a consequence of the heart’s being there.⁶

In a biological context, (1) is most commonly construed in evolutionary terms. How do you explain the traits of living things? If you accept an evolutionary story about the development of living things, you explain at least some of them as things that have been directly selected for, or as the products of such things. In other words, ‘*X* is there because it results in *Z*’ is at least sometimes construed as ‘*X* has been selected for *Z*’. So, for example, ‘eagles have talons because they help eagles catch prey’ is construed as ‘talons have been selected for catching prey’.

Even in biological contexts, this approach has had its critics — some have, for example, claimed it does not fit ecological contexts well — but it seems tolerably clear now that functional explanations of biological phenomena are a respectable kind of causal explanation, that involves

⁵ It might appear that clause (2) rules out the possibility of functional redundancy in the systems that produce *Z*. We would want it to be the function of *X* to *Z* even though, if *X* fails, *Z* will be produced by other things. I think this worry can be met if we see this formulation as a counterfactual generalization about causal relationships. In some cases, *X* can be absent and *Z* can be caused by other factors, but in these cases, if *X* were present and the other *Z*-producing factors absent, *X* would still produce *Z*.

⁶ Wright (1973) is the first explicit account of the aetiological approach to biological function. Still, the basic idea appeared in earlier work, though not spelled out in the same detail. Mayr’s 1961 concept of a ‘genetic ultimate cause’, captures much the same notion.

referring forward in time to the effects that an item is supposed to have but also back in time to a causally explanatory selection process by which the item acquired the effects that it is supposed to have (Neander 1991).

3.1.2 Working through the details

A well-articulated aetiological characterisation of biological function is developed by Godfrey-Smith (1994, p.359) in the following terms:

The function of *X* is to *Z* iff:

- (i) *X* is a member of family *T*;
- (ii) members of family *T* are components of biologically real systems of type *S*;
- (iii) among the properties copied between members of *T* is property or property cluster *C*, which can do *Z*;
- (iv) one reason members of *T* such as *X* exist now is the fact that past members of *T* were successful under selection in the recent past, through positively contributing to the fitness of systems of type *S*; and
- (v) members of *T* were selected because they did *Z*, through having *C*.

Let's see how this works with the eagles and their talons.

- (vi) The talons of Ephialtes the eagle are a member of the family of sets of talons in one of the lineages of eagles of which Ephialtes is a member ('Ephialtes lineage');
- (vii) the sets of talons in Ephialtes' lineage are components of eagles (which are biologically real systems);
- (viii) among the properties copied between the sets of talons in Ephialtes' lineage (admittedly via the 'bottleneck' of Ephialtes' zygote) is the property of being able to grasp prey;
- (ix) one reason sets of talons in Ephialtes' lineage exist now is the fact that past sets of talons in Ephialtes' lineage were successful under selection in the recent past, through positively contributing to the fitness of eagles; and
- (x) the sets of talons in Ephialtes' lineage in the recent past were selected over other variants in the population because they grasped prey.

So a function of Ephialtes' talons is to grasp prey, which seems like the right result.

We should note at this point that it is clear that some molecular genes have biological functions in this sense. For example, it is intuitively plausible that a function (perhaps not the only function) of the *bicoid* gene in *Drosophila* is to set up the anterior-posterior axis in the early embryo. Mutant embryos have no head or thorax and develop tail structures at the head-end (Burglin 2006). They do not survive and reproduce.

This example fits Godfrey-Smith's formal definition:

- (xi) *X* (the *bicoid* gene in Philemon the fly) is a member of *T* (the family of *bicoids* in one of the lineages of organisms of which Philemon is a member ('Philemon's lineage'));
- (xii) the members of *T* are components of biologically real systems of type *S* (the organisms in Philemon's lineage);
- (xiii) among the properties copied between the members of *T* is property *C* (the capacity, in normal developmental circumstances, to set up the anterior-posterior axis in *Drosophila*), which can set up the axis;
- (xiv) one reason the *bicoids* in Philemon exist now is the fact that *bicoids* in Philemon's lineage were successful under selection in the recent past, through positively contributing to the fitness of the organisms in Philemon's lineage; and
- (xv) the *bicoids* in Philemon's lineage were selected because in normal developmental circumstances they set up the anterior-posterior axis in the organisms in that lineage.

There are a few things to note here. First, the members of *T* are conceived of as possessing a property *C* which is passed from one member of *T* to the next and which enables members of *T* to do *Z*. In some cases this may be the best way of describing the relationship between a member of *T* and *Z*. In other cases — and the case of the *bicoid* gene may be one such — there may not be a single obvious property by virtue of which the member of *T* does *Z*. There may be a complex causal chain linking a *T* with *Z*, or the physical makeup of a *T* may directly imply that it is able to do *Z*, without need for an intermediate property like *C*. In the case of the *bicoid* gene, in (viii) above, I have identified *C* as merely 'the capacity, in normal developmental circumstances, to set up the anterior-posterior axis', that is, the capacity to do *Z*.

Second, Godfrey-Smith's formulation of the notion of a biological function includes the requirement that 'among the properties copied between members of *T* is property or property cluster *C*, which can do *Z*'. The 'among' makes it sound as though, in most cases, there are many properties copied between members of *T*, each of which can do something, so that each member of *T* has more than one function. This may often be the case — and there is no doubt that pleiotropy is commonplace among molecular genes — but need not be. In some cases, the members of *T* may have done only one thing that has contributed to the survival and reproduction of the *Ss* and so may possess only one function.

Third, the function of the *bicoid* gene is what its ancestors have done in normal circumstances, that is, in those circumstances where they have done something that has contributed to the fitness of the organisms of which they are a part. No-one thinks that the *bicoid* gene makes anything all by itself. It is entirely dependent on having the right surroundings before it can perform its function. This is true of all things with functions: their capacities generally, including their functions, are dependent on the system in which they are embedded. That does not mean that they do not genuinely possess capacities or functions (just as talons do not do anything all by themselves).

Despite these qualifications, it is tolerably clear that the *bicoid* gene in *Drosophila* has a biological function and the same analysis can be performed for any of the thousands of molecular genes whose selected-for contribution to the survival and reproduction of their host organisms has been reliably established. Such molecular genes have aetiological functions, just as organs or other sub-organismal systems often do.

3.1.3 Other accounts of function

While we are adopting an aetiological characterisation of function in this essay — because that is the best suited to the kinds of biological case that we will be considering — there is no reason why a teleosemanticist needs to restrict function to aetiological function underpinned by natural selection. Both Papineau and Millikan allow aetiological function to be underpinned by cultural mimesis so that words, sentences and other human cultural productions can acquire functions, and hence representational content, by being copied from one person to another, in the same way as inherited traits acquire their functions by being (indirectly) copied from parent to child.

Indeed, there is no reason why we could not have a teleosemantic theory where the function of *X* is construed as the contribution that *X* currently makes to a contemporary goal of a larger system, although I am not aware of any well worked out theory along these lines.

For example, we could, perhaps, construct a teleosemantic theory of representation in which the function from which a token acquires its representational content is characterised, *à la* Cummins (1975, p.762), by reference to its role in an analytical account of a particular capacity of a containing system.

- o Cummins characterises functional explanation as the union of two explanatory strategies.
 - We can explain X 's disposition to Z , if we can find some feature of X that allows us to explain its Z ing as an instance of a more general law (or laws). If we cannot do this, we may be able to analyse Z in terms of other dispositions, $Z_1, \dots, Z_n$, so that if X manifests the Z_i in the right way — maybe in the right temporal order, in the right intensities, or with the right relationships holding between them — X is manifesting Z . Then if we can explain each Z_i in terms of more general laws, we have a unified account of X 's disposition to Z .
 - He then says that the function of X_i in a system S is to Z_i if our analysis of some capacity of S appeals to the fact that X_i has a disposition to Z_i in S . Function, then, is relativised to an account of the capacities of a larger, containing system. For example, the heart's function in the circulatory system is to pump blood because our analysis of the circulatory system's capacity to transport food, oxygen and wastes appeals to the fact that the heart is capable of pumping blood.
- o A teleosemantic account of representation that relies on a Cummins account of function would appeal to functional statements like, 'in the presence of an eagle it is the function of a vervet to produce an eagle cry (because our analysis of the behaviour of a troop of vervets appeals to the fact that vervets are capable of producing eagle cries in the presence of eagles)'.

There would be problems to be overcome. For example, the fact that Cummins relativises the function of an entity to any interesting capacity of the containing system suggests that some work would need to be done to avoid a promiscuous multiplication of functions and contents. Still, the project is not clearly doomed.

Alternatively, we could adopt Bigelow and Pargetter's (1987) propensity account of functions, which takes a function to be disposition apt for selection; so that the biological function of a trait is a disposition to contribute systematically to the survival and reproduction of the organism that possesses the trait in its natural habitat.

As it happens, I agree with Neander that this account is unsatisfactory because it entails that talk of the function of a currently existing item involves no implicit reference to past causes, only future causes, and cannot therefore explain the existing item, only future items. As she says (1991, p.464), ‘When we say that koalas have pouches to protect their young, we take ourselves to be explaining why presently existing koalas have pouches, not why future generations of koalas will have pouches.’

But if we *did* accept such an account of function, we could still use it to underpin an account of representational content. We could say that the cry of an existing vervet means that an eagle is in the offing just in case the disposition to that behaviour will contribute to the survival and reproduction of future vervets (and perhaps, of the existing vervet in future eagle situations). We could also adopt a more general Millikanish account of representational content in which dispositional functions adapt consumer and producer devices to work together in future in a way that supports the survival and reproduction of the consumer.

So far as I can see, the fact that teleosemantic theories have, to this point, used a selective theory of function is more a contingency of intellectual history than an intrinsic features of such theories. Millikan presented the most complete early teleosemantic theory and she used a selective notion of function. Later people have followed her example. Moreover, one of the explanatory benefits of teleosemantics is that it brings representation in the full range of biological contexts into a single continuum (see section 9.5) and, in an effort to get clear on the foundations of the theory, much of the discussion in the literature has focused on relatively basic examples in the realm of animal signaling. For these examples, a selective theory of function is entirely adequate. If attention turns to more complex examples in human languages, where the selective histories of the producer and consumer devices are far less clear, we may find that other, more flexible notions of function have more appeal.

3.2 Function and representation

However we decide to characterise the notion of function, it is obviously not the case that anything with a biological function bears representational content. My heart has at least one function (pumping blood around my body), my thumb has at least one function (holding things), my CGU codons have at least one function (acting as a template for the synthesis of arganine), the *let-60* gene in *C. elegans* has at least one function (determining vulval cell fates in the larva,

in cooperation with other developmental resources).⁷ My heart and my thumb do not represent anything but do my CGU codons? Does the worm's *let-60* gene? Does the expression of that gene?

3.2.1 Representation as covariation

Teleosemantic theories try to characterise representation in terms of the functions of the entities involved. And this turns out not to be any sort of straightforward enterprise. What then must the functions of a system be in order that it (or something it produces) represents some state of affairs?

A simple, permissive answer is that it must be the function of the system to covary with particular states of affairs.

For example, the diameter of my pupil covaries reliably with the brightness of the light in its vicinity. And it seems pretty certain that it is the function of my pupil to narrow or widen with the brightness of the light: it is not just that narrow pupils are usually caused by bright light as smoke is usually caused by fire. The fact that previous fires have produced smoke doesn't explain why contemporary fires do — it is not the function of a fire to produce smoke — but the fact that previous pupils have contracted in the presence of bright light does, at least in part, explain why contemporary pupils do. When pupils in previous generations have not contracted in bright light, the associated retinas have been damaged and the chances that the containing organisms will survive and reproduce have been reduced.

So we may take it that it is the biological function of the pupil to covary (in its dilation) with some state of affairs in the world (the amount of ambient light) and the pupil's ancestor pupils have been selected for because

- o (inter alia) they have covaried with those states of affairs; and
- o the way they have covaried with the environment has had causal effects that have aided their survival and reproduction.

⁷ I do not mean cooperation in any intentional sense here, merely that the *let-60* gene has been selected, along with other genes, as part of a system (which includes non-selected developmental resources) that forms the vulva in normally developing worms.

Another example might be the reflex that causes people to flinch from extreme heat. It is the function of the reflex mechanism to respond to extreme heat in the environment. The mechanism helps the containing organism survive and reproduce by protecting it from damage, and hence the mechanism helps itself survive and reproduce by way of the organism.

Is this representation of any kind?

It is tempting to say that it can be the function of system X to respond to some feature of the environment — and in a way that makes a causal contribution to the survival of X (perhaps by making a beneficial causal contribution to some larger system, like an organism, of which X is a part) — without either X or its response being a representational system or part of one.

At the least, we can say at this point that this kind of system, if it bears representational content at all, bears only the *most* basic type of representational content.

- o There is no communication going on here: a core characteristic of representational tokens in paradigmatic representational systems (natural languages, mentalese, vervetese) is that, at least sometimes, they are used by some sort of consumer device to guide its behaviour. A natural language utterance affects the behaviour of the hearer; the conclusion of an inference in a person's head triggers action; a vervet call affects the behaviour of other vervets. There's none of that going on here.
- o There is no storage of information involved here: the response to the stimulus is instantaneous. Core intuitions about paradigm representational systems are that a representational token is some kind of surrogate of the state of affairs that it represents, and that some system can store the token to deal later with the represented state of affairs. Some tokens cannot be stored themselves, e.g. the sound waves in air that constitute a spoken utterance, but in more sophisticated systems an evanescent token like the spoken word can be transformed into a longer lasting token, e.g. the (not very well understood) neuronal patterns that constitute memory tokens in the human brain. And, as I shall argue later, genetic clocks register the passage of time. Simple immediate responses like that of the pupil displays no such 'memory'.
- o There is no plasticity of response: the pupil contracts when there is more light around and dilates when there is less. The covariation is one dimensional.

3.2.2 Adapting the behaviour of a consumer device

How can we expand a functional account of representation beyond this kind of rigid stimulus-response example? And how can we distinguish between functions that underpin genuinely representational tokens and other functions to respond to environment circumstances?

An example from Clark and Wheeler (1996, p.9) provides a jumping off point. Consider a robot arm that is designed to reach out and grip a cog. An explanation of how it does this may mention the force of gravity, a spring-loaded assembly in the arm and a set of instructions for reaching in the relevant context.

It is not the function of the force of gravity to respond to the environment and that serves to distinguish it from both the assembly and the instructions: it certainly isn't representing anything. While both the assembly and the instructions do have the function of responding to the environment in a way that helps the overall system grip the cog, the assembly can hardly be thought of as representing the gripping of the cog, while the instructions plausibly can.

What's the difference between the assembly and the instructions? One possible difference is that the instructions are for reaching out and gripping *in the relevant context*. They control the assembly and cause it to grip or not to grip. And the instructions cause the assembly to grip only (or at least mostly) in the relevant context. Of course it might be a poorly designed robot and the assembly might actually grip only in a minority of instances of the relevant context, generating plenty of 'false negatives'. Or it might grip in only some instances of the relevant context (that is, it generates false negatives) but might also grip in many circumstances which are not instances of the relevant context (that is, it also generates many false positives). But we could still say that the instructions represent the gripping of the cog because it is the function of the instructions to adapt the activity of the assembly to the relevant context, even if it only rarely performs that function.

The robot is an artefact, of course, and it gets its functions derivatively from the intentions of the people who design, build and use it. Exactly how artefacts get their functions is a question in itself but not one that we need to explore in this essay: the idea exemplified by the robot scenario works when the functions of the systems we are talking about are not conferred by a human designer but by natural selection.

Instead of gravity, the arm assembly and the instructions, consider gravity, wind resistance, an eagle's talons and the perceptual and motor control mechanisms in the eagle's head (let's call them collectively, the tracking mechanism). Again, the force of gravity and the wind resistance that the eagle encounters haven't been selected for, have no functions and certainly aren't

representing anything. It seems that it is the function — or at least one function — of both the talons and the tracking mechanism to grip the fleeing rabbit, so at least they're both in the running. But it is only the tracking system that has as its function to adapt the activity of the talons (and wings and other bits) of the eagle to the fleeing rabbit.

So we might think that some states of the tracking mechanism or some (neuronal) signals generated by the tracking mechanism represent the fleeing rabbit while, say, the extension or clasping of the eagle's talons does not.

3.2.3 Papineau

Papineau uses these functional ideas to set out a more demanding account of representation, focusing primarily on human beliefs and desires. According to him (1984), the content of a desire is its satisfaction conditions and the satisfaction conditions are the effects that it is the desire's biological function to produce. Like most teleosemantic theorists, Papineau takes an aetiological view of function under which the function of a desire is derived from the selective histories of the mechanisms that generate it (see section 3.1 above).

So, for Papineau, the *function* of the desire to drink is to induce me to rehydrate myself because the mechanism in me and my ancestors that has generated the desire to drink has been selected for inducing me and my ancestors to rehydrate themselves.

By extension, the *content* of my desire to drink is that I drink non-toxic, rehydrating liquids because its function is to induce me to do so. It is not the content of my desire that I drink sea water because it is not its function to induce me to do that. Why is that not its function? Because it is not when the desire has prompted me or my ancestors to drink sea water that it has contributed to our survival and reproduction — it is when the desire has prompted me or my ancestors to drink non-toxic, rehydrating liquids.

The content of a belief is determined by reference to the content of desires with which it is its function to interact. The function of a particular belief is to prompt actions (on the part of an organism) which will succeed in satisfying some current desires of the organism only if particular circumstances obtain. The truth conditions of the belief, then, are those circumstances, that is, the circumstances in which it is the function of belief to combine with current desires in such a way as to prompt behaviour that results in the satisfaction of the desires.

There are two problems with Papineau's account that make it difficult to accept as a general account of representation.

First, it is not clear that beliefs and desires are members of reproductively established families and are also components of biologically real systems, as our ‘modern history’ account of function requires. Remember that:

The function of *X* is to *Z* iff:

- (i) *X* is a member of family *T*;
- (ii) members of family *T* are components of biologically real systems of type *S*; ...

Is a desire *X* actually a member of a family of desires *T*? Desires are certainly not reproduced directly — one desire to drink hydrating liquids is not reproduced from a similar previous desire — so they do not form part of a first order reproductively established family. It does, however, seem likely that desires to drink hydrating liquids are generated by the same devices and these devices, to the extent that they are reproduced through the genome, probably do form a reproductively established family, so that the desires they generate probably do form a higher order reproductively established family. So far, so good for Papineau.

Still, there is a second problem for Papineau: how can desires be differentiated from other states of an organism that have biological functions. If we know that something is a desire, we can work out its content by reference to its functions — its satisfaction condition is the effect which it is the desire’s function to produce, but it is not at all clear how we are meant to tell whether we have a desire in the first place.

For example, it is a function of the spleen to remove old red blood cells from the blood. One effect that it is the spleen’s function to produce is blood free of senescent erythrocytes. But neither the spleen nor any of its activities is a desire and blood without old red cells in it is not the satisfaction condition of any desire. If we identify the content of a belief by reference to the desires with which it combines to produce successful actions, the difficulty in identifying desires extends to the identification of beliefs as well. If:

- o we do not have any clear way of distinguishing between desires, which have representational functions, and other biological systems, which have functions of different kinds; and
- o we identify beliefs at least in part by reference to the desires with which they interact; then

we also have no clear way of identifying beliefs — i.e. there is no clear way of using Papineau's machinery to analyse the subsystems of organisms.

Millikan's account of representation (section 3.2 below) escapes this difficulty because she characterises an intentional icon in terms of a more specific kind of functional structure. If something is to be an intentional icon, its function must be to mediate between a producer device and a consumer device, the presence and proper functioning of each being a 'Normal' condition for the proper functioning of the other — so that the 'component of a biologically real system' requirements is satisfied. In the case of an imperative intentional icon, it is the proper function of the consumer to respond to the icon by producing a state of affairs onto which the icon will map. It is the notion of mapping, which Papineau does not employ, that makes the difference between representational tokens and other items with aetiological functions and thus allows Millikan to get out of this bind: the spleen is clearly not intentional on her account.

Still, although Papineau's account has some problems, it clearly has enough in it to ground a significant objection to the claim that, on a teleosemantic view of representation, nucleic acid structures bear representational content. His doubts (2003, p.121) arise because he thinks that while it is the function of molecular genes to produce certain proteins in appropriate circumstances — and, arguably, that it is their function to contribute to particular phenotypic traits — 'there is nothing in this akin to the gearing of these causal sequences [the causal sequences involved in transcription, editing and translation] to variable environmental circumstances.'

As I shall argue later in this essay, I think Papineau is too pessimistic here. The causal sequences involved in protein synthesis are very often triggered by environmental circumstances (see section 4.3). Molecular genes for the production of hundreds of enzymes and gene regulation proteins are expressed in response to changing conditions in the cellular environment and in the environment external to the organism.

For example, in the drinking case, the desire to drink is geared to variable environmental circumstances inside my body. If the concentration of salt in my body exceeds some threshold beyond which damage to my tissues is likely to ensue, this activates osmoreceptors in my subfornical organ, one of three small 'interventricular organs' near the top of the brain stem. The activation of the osmoreceptors excites higher integrative centres in my brain where my conscious experience of thirst arises (McKinley and Johnson 2004). My desire to drink is geared to environmental conditions — specifically, salty conditions — inside my body.

Papineau's characterisation of content focuses on representation inside the human brain; he is primarily concerned with how our beliefs and desires manage to bear representational content. Since we do not know all that much about how our beliefs and desires are produced and consumed within the brain, it might be his focus on human thought that led Papineau to focus more on the function of the representational tokens themselves — the particular beliefs and desires — and less on the functions of the mechanisms that produce and consume them.

Millikan, Shea and others characterise representation in terms of the functions of the systems that produce and consume representational tokens. In particular, they require that the functional structure that characterises representation include functions to affect the activity of some consumer device.

3.2.4 Millikan

Millikan (1984, p.96) puts some theoretical flesh on the bones of this intuition in her definition of an intentional icon:

- (1) An intentional icon is a member of a reproductively established family with direct proper functions.
- (2) Normally, an intentional icon mediates between a producer device and a consumer device, the presence and proper functioning of each being a Normal condition for the proper functioning of the other.
- (3) Normally the intentional icon adapts the consumer device to conditions in such a way that the consumer device can perform its functions.
- (4) In the case of an imperative intentional icon, it is the proper function of the consumer to respond to the icon by producing a state of affairs onto which the icon will map.
- (5) In the case of an indicative intentional icon, 'the Normal explanation of how the icon adapts the interpreter device such that it can perform its proper functions makes reference to the fact that the icon maps onto something else'. In other words, it is the function of the consumer to respond to the icon in some particular way and it cannot do this, at least not Normally, unless the icon maps onto something else.

A number of terms in this account warrant some explanation. Millikan (1984, p.23) characterises a ‘first-order’ reproductively established family in this way:

Any set of entities having the same or similar reproductively established characters derived by repetitive reproductions from the same character of the same model or models form a first-order reproductively established family.

So the tokens of a particular molecular gene in a lineage of ocelots form a first order reproductively established family because they are directly reproduced, each item from the previous item in the lineage. A higher order reproductively established family consists of items produced by the members of a reproductively established family (whether or not first order) when it is the function of the family to produce such items. So all the livers in a lineage of ocelots form a higher order reproductively established family (but not a first order reproductively established family, because a particular liver is not copied *directly* from the previous liver in the lineage).

‘Direct proper function’ is essentially the notion of biological function discussed in section 3.1 above.

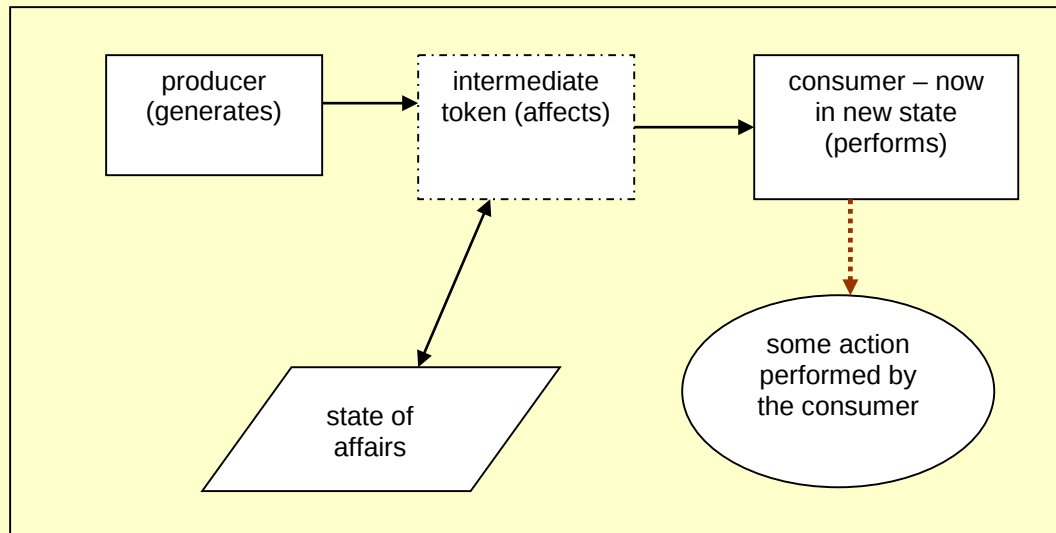
‘Normally’ means in the kinds of circumstances in which a system with a biological function and its ancestors have performed that function.

Clearly a lot hinges on the concept of mapping and Millikan provides us with the following characterisation: an intentional icon *X* maps onto a state of affairs *Y* iff:

- o the relationship between *X* and *Y* follows a mapping rule;
- o according to the mapping rule, a ‘critical mass’ of icons and states of affairs have entered into correlation patterns;⁸
- o consumer devices have responded systematically to these patterns; and
- o these responses explain their successes, i.e. the responses have contributed to the survival and reproduction of consumer devices.

⁸ Millikan uses ‘affairs in the world’ where I use ‘states of affairs’.

Figure 5: A Millikan-style imperative intentional icon



An important characteristic of this account of an intentional icon is that intentional icons in the same family can possess representational content even if the members of the family have rarely succeeded in effecting communication between consumer and producer. The ‘critical mass’ referred to above need not be a large proportion of the total number of signals emitted, provided the stakes are high enough. So, for example, most predator alarm calls emitted by squirrels are emitted when no predator is actually in the offing (Wilson and Hare 2004), but provided that squirrel calls and the presence of predators have been sufficiently correlated in the evolutionary past, the calls still count for Millikan as intentional icons.

It might be useful to see how all this fits together in a real life example of animal signaling. One of Millikan’s favourite examples is the bee dance. Bees dance in particular ways that signal to other bees where pollen is to be found. Such a bee dance is an intentional icon because:

- (1) It is a member of a higher order reproductively established family. Bee dances are not copied directly from generation to generation but the molecular genes whose function it is to produce the mechanisms that produce the dance are copied in this way.
- (2) When a bee dances in Normal circumstances — i.e. the circumstances in which, in the past, bee dances have helped bees survive and reproduce:
 - o the dance mediates between a producer bee and a consumer bee; and

- o both bees have to be present if either is to fulfill its function. If there's no dancing bee, there's no signal produced for the watching bee and if there's no watching bee, the dancing bee dances in vain.
- (3) In Normal circumstances, the dancing bee adapts the behaviour of the watching bee in such a way that the watching bee can perform its function, i.e. can find pollen.
 - (4) The dance can be taken to be an imperative intentional icon because it is the proper function of the consumer bee to respond to the dance by flying in the direction and distance indicated by the dance (i.e. by producing a state of affairs onto which the dance maps). There is a mapping rule linking bee dances and the location of pollen sources because over evolutionary history a critical mass of dances and pollen sources have been linked by correlation patterns. In the case of bee dances the pattern depends on the number of waggles (indicating how far away the pollen is) and angle of the bee relative to the sun while wagging (indicating the direction of the pollen). Researchers have 'decoded' the bee dance to reveal the correlation patterns between these attributes of the dance and the location of the pollen that has been found by the dancing bee (Veeraraghavan, Chellappa et al. 2008).

We could also take the dance to be an indicative icon in Millikan's terms. Many simple signaling icons are what Millikan calls 'pushmi-pullyu' icons: they are imperative and indicative at the same time.

3.2.5 Imperative, indicative and pushmi-pullyu

A fundamental distinction for any theory of representation is the distinction between indicative and imperative representations. Happily, a teleosemantic approach to representation can deal with this.

A purely indicative icon is an icon that has the function of mapping onto a state of affairs — in Millikan's correlation-based sense of mapping (see section 3.2 above) — but does not have the function of producing particular behaviour in a consumer device. For example, if Arsinoë says to Berenice 'here comes a lion, it is not the function of the utterance, or of the mechanisms that produce it, to induce any particular behaviour in Berenice. If she is carrying a flaming torch or a spear, running away from the lion may not be the best response: brandishing the torch or standing her ground with the spear are probably better. If she is a wildlife photographer in a lion-proof

hide, photographing the animal may be the way to go. But regardless of Berenice's specific circumstances, the utterance, an intentional icon in Millikan's sense, maps onto the approach of the lion because:

- o the relationship between Arsinoë's utterance and the approach of the lion follows a mapping rule;
- o a critical mass of utterances of 'here comes a lion' and the approach of lions have entered into correlation patterns;⁹
- o hearers have responded systematically to these patterns (though in this case the responses will not have followed simple stimulus-response patterns); and
- o these responses (which will in this case have varied depending on other environmental circumstances) have contributed to the survival and reproduction of the hearers.

A purely imperative icon is one whose function it is to produce particular behaviour in the consumer device regardless of what states of affairs obtain. For example, if Arsinoë says to Berenice, 'throw a rock at the lion', it is not the function of the utterance to map onto a particular state of affairs, or of the producer devices to produce a token that does so. It is the function of the utterance to induce Berenice to throw a rock at the lion.

The functions of purely indicative and purely imperative icons are adapted to one another, in the sense that a representational system — a producer-token-consumer system — must have both kinds of icon and each kind of icon must perform its function if the consumer device is to succeed in dealing with the environment. Purely indicative icons map onto the world but lack a means of inducing actions on the part of the consumer. Purely imperative icons induce actions on

⁹ For ease of exposition, I have somewhat simplified Millikan's account here. Many sentence tokens are the only tokens of their type that have ever existed: so if I say 'I am going to Alkippe's birthday party at the Ainslie pub next Friday and I'll be eating the fantastic squid stew', that is probably the only time that sentence has ever been uttered. Millikan deals with this 'novel utterance' issue by ascribing to the different semantically significant features of a sentence, including adapted functions, the function of collaborating with other linguistic features. For example, it is the function of the aoristic past tense to pick out events that have occurred before the time of the utterance and to combine with other features to pick out different kinds of states of affairs.

the part of the consumer device but lack a means of ensuring that those actions are performed in the appropriate circumstances.

As Papineau notes in relation to beliefs and desires, the two kinds of icon, performing their functions in concert, can succeed in adapting the consumer's behaviour to the environment so as to support its survival and reproduction. And of course, once we have imperative and indicative icons, we have the raw theoretical materials for belief-desire psychological explanation. Why did Alcibiades go to the gym? Because he wanted to wrestle Bias and he believed that Bias would be at the gym.

In simpler representational systems, though — including many of the genetic systems we will be considering in this essay — the distinction between imperative and indicative representational tokens may not be so clear cut. Millikan identifies a more primitive kind of intentional icon, which is both imperative and indicative at the basic functional level (1995, p.190).

Consider the food call of a hen to its chicks. It seems reasonable to assume that the function of the mechanism that produces the call (and the proper effect of the call itself) is to get the chicks to come to the mother and eat. Its function is to adapt the behaviour of the consumer device, the chicks. On the other hand, it can only perform that function if there is food with the mother when she makes the call. So it seems that it is the function of the food call:

- o to map onto the presence of food with the mother; *and*
- o to induce the chicks to come to the mother.

Another example from the realm of animal signaling is the 'monkey see, monkey do' cells in the inferior premotor cortex of macaque monkeys (Rizzolatti, Carmada et al. 1988). These cells fire in a particular pattern depending on the manual manipulation which the monkey is about to perform and in the same pattern when the monkey sees another monkey performing that manipulation. So the function of these cells appears to be, simultaneously, both:

- o to map onto the manipulation being performed by the other monkey; *and*
- o to induce the monkey's motor systems to perform the same manipulation.

A final example could be imitative behaviour in very young infants where there does not seem to be any distinction between the baby's behavioural system:

- o representing a state of affairs (e.g. the mother holding her ear); and

- o adapting the behaviour of the baby to that state of affairs.

In such cases, it is the function of the producing system both to map onto the state of affairs and to adapt the consumer device to it; and to perform these functions at the same time by means of the same physical process.

We should note two important differences between representational systems that generate both imperative and indicative icons and a system that generates only pushmi-pullyu icons. The distinction is of importance not only because it is a necessary aspect of a general theory of representation that can account for the different attributes of representational systems that arise across the biological world, but also because it will turn out that many cases of representation in the genome are of the pushmi-pullyu kind.

First, systems of the former kind are capable of inference, broadly construed. In other words, when the consumer device receives a token, the way the token impacts causally on the consumer device and the response, if any, that the token elicits from the consumer device depend on the content of other representational tokens that the consumer has already received or, in the case of more sophisticated consumer devices, representational tokens that the consumer has generated internally.

An example of a very simple system that could reasonably be said to perform inference is one where:

- o the producer device produces a series of *A* tokens or *B* tokens,
- o the consumer device does nothing unless it receives two *As* in a row, in which case it does *R*.¹⁰

Of course, in humans and animals, inference is much more complicated:

- o The range of tokens that can be produced by the producer device is as good as infinitely large.

¹⁰ One might argue that this is more a matter of priming than inference: the first *A* token lowers the threshold for a following *A* to elicit an *R*. But I am not sure that some inferences in more sophisticated systems function very differently: if Arsinoë says to Berenice, ‘Snakes are very dangerous’, that lowers Berenice’s threshold for snake-fleeing behaviour.

- o The range of responses available to the consumer device is also very large.
- o The way that different tokens affect the responses of the consumer device depends in complicated ways on the tokens that have already been received. In the example in the previous paragraph, the state of the consumer device can distinguish only two states of affairs — one where the last token received was an *A* and one where it was a *B*. A human being combines tokens received from a diverse sensory apparatus to maintain some kind of internal model of the world and it is only when the model reaches certain states — for example, where some sort of threat gauge reaches a certain point — that particular actions are triggered.

In a more complex inferential system, between inputs from producer devices or from the environment and the behavioural output of the consumer, there are causal processes whose function it is to keep the internal model mapping onto the environment in Millikan's sense — not that they will always succeed in performing these functions. These processes adapt the consumer device to respond successfully if further tokens are received from the producer or if particular environmental conditions arise.

Inference may be deductive, inductive or abductive. Whatever the case, representational tokens are stored and combined causally with other tokens (newly arrived representations, mostly, i.e. tokens newly generated by a producer in response to some environmental conditions) to produce further tokens, which have some indicative or imperative function.

Second, the responses of pushmi-pullyu systems are less flexible than the responses of indicative-imperative systems. In a pushmi-pullyu system, for example, you cannot note the presence of food without modifying behaviour in a specific way, or vice versa. To put it another way, with pushmi-pullyu representation there is only one response per signal. Whenever a vervet receives an eagle call, the function of the call is to induce the vervet to look into the air. There is a one-to-one relationship between a signal and the response that it is the function of the token to evoke.

A pushmi-pullyu system can still be relatively flexible in its responses, in the sense that it could be able to respond to a large number of different inputs, or sets of inputs, at a particular time. Vervets do not actually do this, but in principle there could clearly be a system of predator cries that includes one for 'there's both an eagle and a snake in the offing' or a system where the producer vervet emits an eagle cry and a snake cry in quick succession and the consumer vervet responds in a particular way that helps it deal with the combined threat. In the first case it seems natural to describe the consumer as responding to a single signal and in the second as responding

to an array of different signals. But either case will still constitute a pushmi-pullyu representation provided that its functions include both mapping onto a state of affairs and adapting the behaviour of the consumer to that state of affairs.

As will become clear, I think that most representation on the genetic level falls into the pushmi-pullyu category.

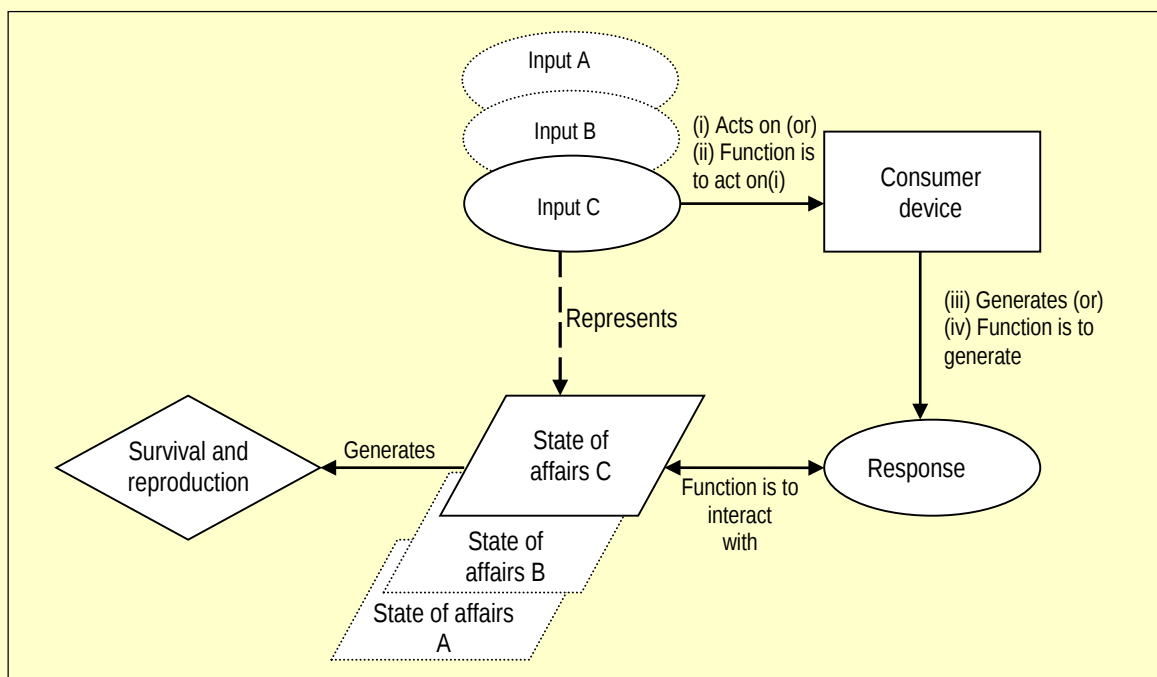
3.2.6 Jablonka and the consumer

A Millikan-style characterisation of representation requires that a token with representational content be produced by a system whose function it is to produce tokens that will interact with a particular kind (or particular kinds) of consumer device but it is worth noting that other theorists have tried to develop teleosemantic accounts of representation that do not require the producer of the token to be performing a biological function in order for it to bear representational content.

In particular, Jablonka (2002) argues that the input can be an entirely non-semantic phenomenon, as well as a signal that has itself been selected for, or a signal produced by a mechanism that has been selected for (see Figure 6).

So a black cloudy sky, when perceived by a human or some other animal that ‘knows’ cloudy skies mean rain, does indeed mean rain.

Figure 6: Jablonka's consumer-centred model



So for Jablonka, the processes that generate representational content are going on inside the consumer device. For Millikan and Papineau (and Shea), it is the relations between producer, token and consumer that generate representational content. One might speculate that two-sided Millikanish systems evolved from one-sided Jablonka systems, as consumer responses to producer behaviour gradually exerted selective pressure on producer lineages.

Jablonka says that representation arises when the consumer responds to some input in a ‘functional’ way — that is, in a way that improves its chances of survival and reproduction. Her explicit definition of biological information is:

A source—an entity or a process—can be said to have information when a receiver system reacts to this source in a special way. The reaction of the receiver to the source has to be such that the reaction can actually or potentially change the state of the receiver in a (usually) functional manner. Moreover, there must be a consistent relation between variations in the form of the source and the corresponding changes in the receiver. (Jablonka 2002, p.582)

If we take this literally, and say that in any particular case, representation arises only if the input is *actually* interpreted by a consumer, we end up with quite implausible results.

- o If I call out ‘I’m over here, on top of the Doric column’, my call means that I am on top of the column only if someone hears me.
- o If a beaver sees a wolf and slaps the water with its tail, the slaps bear information about the proximity of a predator only if another beaver senses the slaps and takes evasive action. If there are no other beavers around, the slaps mean nothing. Even less plausibly, if there is another beaver around but, suffering from depression, it does nothing in response to the tail slaps, the slaps mean nothing.
- o A cloudy sky has representational content when it’s seen but not when it’s not. So most of the cloudy skies that have ever been have represented nothing but a few — those that have been interpreted as signaling rain on the way, by some of the cleverer apes, or by humans — *have* had representational content.

This cannot possibly be right. A satisfactory account of representational content must be able to contend with misrepresentation and with situations where representations are produced but not consumed.

Jablonka’s words in the second sentence of the quote above are, ‘... the reaction can actually or potentially change the state of the receiver in a (usually) functional manner’, so it is probably

uncharitable to interpret her as requiring that the reaction to the input *actually* induce the consumer device to respond in a successful manner.

Even if, however, we take her as saying that the input has content if it *usually* induces some response by the consumer that helps the consumer survive and reproduce, we must surely be spreading our representational net too widely.

For then natural signs like footprints or scats could ‘have information’ in Jablonka’s sense. If a hunter sees the footprint of a wolf, she can react to this ‘source’ in a special way and her reaction may usually change her state in a usually functional manner. For example, she can run in the opposite direction from the way the footprint is pointing, and this may usually carry her further away from the wolf and this may usually increase her chances of not being eaten. But surely this is missing the distinction between natural information and representational content. A footprint *means* a wolf has been here in the same sense that smoke means fire, or in the sense that a narrow tree ring means the weather was cold the year the ring was formed. But a footprint is not false if no wolf has been here at all.

This is not to say that Jablonka’s definition of biological information is somehow illegitimate. It makes sense of an important class of phenomena, so it certainly has its uses, but it will not serve as a naturalistic account of representational content.

3.2.7 Shea and Price

Shea (2007) accepts the key ‘output’ insight behind Millikan’s view — that the content of representational tokens depends on the effects caused by those tokens — but adds an ‘input’ condition which requires that a token must carry natural information about its content if it is to bear representational content. This gives rise to the following formulation:

A representation of type R has content C if:

- (a) Rs are intermediate in a system consisting of a producer and a consumer cooperating by means of a range of mediating representations (all specified non-intentionally), in which every representation in the range also satisfies (a) to (d);
- (b) Rs carry the natural information that condition C obtains;
- (c) an evolutionary explanation of the current existence of the representing system adverts to Rs having carried information about C; and
- (d) C is the evolutionary success condition, specific to Rs, of the behaviour of the consumer prompted by Rs. (Shea 2007, p.419)

Let's see how this works with the beavers.

Anacreon is a beaver. His tail slaps (a representation of type R) mean there's a wolf about (has content C) if:

- (a) the slaps are intermediate in a system consisting of a producer (Anacreon) and a consumer (Bacchylides, another beaver) cooperating by means of a range of mediating representations (tail slaps, mating advances etc.), in which every representation in the range also satisfies (a) to (d);
- (b) the tail slaps carry the natural information that there's a wolf about;
- (c) an evolutionary explanation of Anacreon slapping his tail adverts to tail slaps having carried information about the presence of wolves; and
- (d) the presence of a wolf is the evolutionary success condition, specific to tail slaps, of diving off the bank into the pool (the behaviour of the consumer prompted by tail slaps).

This is very similar to Price's (2001, p.75) account of intentionality, under which:

a mechanism will count as an intentional mechanism if its function is to control the operation of some second functioning mechanism in such a way as to ensure that the behaviour produced by that second mechanism coincides with a certain condition or set of conditions in the environment.

The main difference is that, in paragraph (a), Shea requires that it is a function of the producer device to produce more than one different kind of token to which the consumer device systematically responds. Price, by contrast, is happy to attribute intentionality to a system that produces only one signal that elicits only one response from the consumer device. Thus Shea might hesitate to say that a frog's tongue snap represents a fly — because the mechanism that produces the snaps produces only the snaps — while Price would not.

This divergence between Shea and Price, while not negligible, is not likely to lead to many different judgements in real cases, where it seems likely that there will be more than one possible signal available. So, for example, it appears that the intensity and persistence of beaver tail slaps bears some content and expands the range of available signals beyond one (Tevis 1950).¹¹

¹¹ In passing, it might be worth noting that we know beavers use anal gland secretions to identify members of their own family. So Anacreon could establish friendly relations with Bacchylides by daubing his

Whether the beaver tail slaps count as representational under Shea's more demanding criteria will also depend on how we identify the producer mechanism.

If we take it to be a sub-organismal system whose *only* function is to produce tail slaps in response to the presence of predators, we would say that Anacreon's slaps are representational under Price's account but not under Shea's.

Whether such a system exists is partly an empirical question but it also raises questions about how we individuate systems within a larger system (like an organism). For example, should we think of the heart as a system on its own or as a part of a larger circulatory system, or both? Is there a single system in humans that generates both imperative and indicative tokens?

I think we can use Millikan's notion of a relational proper function (1984, p.39) to individuate functional systems within organisms. She defines a relational proper function as a function 'to do or produce something that bears a specific relation to something else'. Suppose:

- o we have a system *S* with a number of spatio-temporal parts — e.g. the heart;
- o each of *S*'s parts has a relational function with respect to one or more of the other parts — the aorta, the septum, the tricuspid valve etc. all affect one another's functioning;
- o none of the parts has a function other than a relational function with respect to any other part of *S* — i.e. none of the parts of the heart has a function to do anything on its own; all its functions that relate to other parts of the heart involve working with other parts; and
- o none of the parts has a relational function with respect to any system outside *S* — none of the parts of the heart has the function of producing effects that bear a particular relation to things outside the heart; the 'functional reach' of each part of the heart is restricted to the heart itself.

Then we might say that *S* is functionally self contained in a way that none of its constituent subsystems are and it also seems reasonable to say that effects produced by *S* — e.g. the circulation of blood around the body — are produced by it, but not by any of its subsystems. This looks to me like a pretty good way of characterising systems with functions: it uses notions with

secretions around the local environment — although we would probably not think of the daubing signal as part of the same representational system as the tail slapping.

which we are already familiar from our overall account of function and it seems to capture the idea of self-containment well.

Now, to return to the differences between Shea and Price, it may be that there is no functionally self-contained sub-organismal system that produces only slaps: the narrowest functionally self-contained system that has the function of producing slaps that adapt the behaviour of consumer beavers may also have the function of producing other signals that adapt consumers' behaviour in other ways. In this case, their accounts yield the same answer; it is only if we have a system that produces just one kind of signal that the accounts come apart. In the end, I doubt that a lot hangs on this question. There no real difference between saying that a one-response system is a minimal representational system, and in saying that it is not quite a representational system, but would become one if a little flexibility evolved in the lineage.

Like Price and unlike Shea, Millikan is also willing to attribute a basic grade of representation to very simple signaling systems. In *Varieties of Meaning* (2004, p.158), she says:

The bottom-most level of inner P-P [pushmi-pullyu] signs is ubiquitously exemplified, not merely in neural matter, but in the many chemical messengers found in the body tissues and circulatory systems of animals. ... To suggest that genuine intentionality, genuine aboutness, with the possibility of misrepresentation, actually occurs at this level may at first seem far-fetched. ... These are the most humble sorts of limiting cases of intentionality. By treating such simple signals as intentional signs, just as by treating zero as a number, we will be able to examine their relations to various successors ...

Second, Shea specifies that the function of the producer mechanism must be to cooperate with the consumer and vice versa. I think this is too restrictive — at least if we construe 'cooperating' with any strength at all. It is hard to think of threat displays among hippos, or the deceptive alarm calls that shrikes give to deflect other birds from a food source (Maynard Smith and Harper 1995, p.307), as signals through which different animals cooperate, but they are surely as representational as other animal signals that do have a cooperative function. Rather than insisting on cooperation between consumer and producer, it might be better to require only some overlap of interests. This seems to fit a much wider range of cases that we would surely wish to capture in a teleosemantic account of representation:

- o Hippos do not want to fight unless they have some chance of winning, so although it is not the function of a hippo threat display to elicit cooperation from the other hippo, there is some commonality of interest: both sides want to avoid fights that they would lose at great cost.

- o Deceptive alarm calls are parasitic on genuine alarm calls. The deceptive shrieks rely on the fact that alarm calls often enough signal the approach of a predator.

This broader specification also fits the range of genetic cases that I will be exploring later in this essay. In most cases the function of genetic representation is to elicit behaviour from the consumer that will benefit both producer and consumer, but in some cases — e.g. cases of deception — there is no more than an overlap of interests between deceptive producer and deceived consumer (Skyrms 2010, chp 6). For example, viruses that reproduce by hijacking the replicative machinery of a host cell harm the host, but the success of their strategy relies on the fact that the machinery is not hijacked too often. There is some overlap of interest because, if the host's machinery were hijacked all the time, the host could not survive and the virus would do itself out of a living.

Third, I think we need to construe paragraphs (a) and (b) of the Anacreon analysis above in functional terms. Remember that (a) requires that 'Rs [the slaps] are intermediate in a system consisting of a producer [one beaver] and a consumer [a second beaver] cooperating by means of a range of mediating representations'. The whole point of teleosemantics is that the content of the slaps is dependent on their function (or at any rate some functional structure in which they participate), so we cannot reasonably construe Shea's condition (a) as requiring that some particular slaps are actually consumed by a cooperating beaver before they can possess representational content. This would mean that unconsumed slaps have no content and we would surely wish to say that they do possess content, just as an eagle cry emitted by a vervet possesses content even if unheard by any other vervet or a human cry for help possesses content even if no one hears it. The natural way to construe Shea's condition (a) is that:

- o it is the *function* of the mechanism in Anacreon that generates these particular tail slaps to generate tokens that fulfill the conditions listed in (b) to (d); and
- o it is the *function* of the interpreting mechanism in Bacchylides to generate a response to the slaps that fulfills the condition given in (d).

Similarly, we need to construe (b) — 'Rs carry the natural information that condition C obtains' — as 'it is the function of Rs to carry the natural information that C obtains'. At any rate, I do not think we can insist with Shea that the Rs must *actually* carry the natural information that C obtains (Shea 2007).

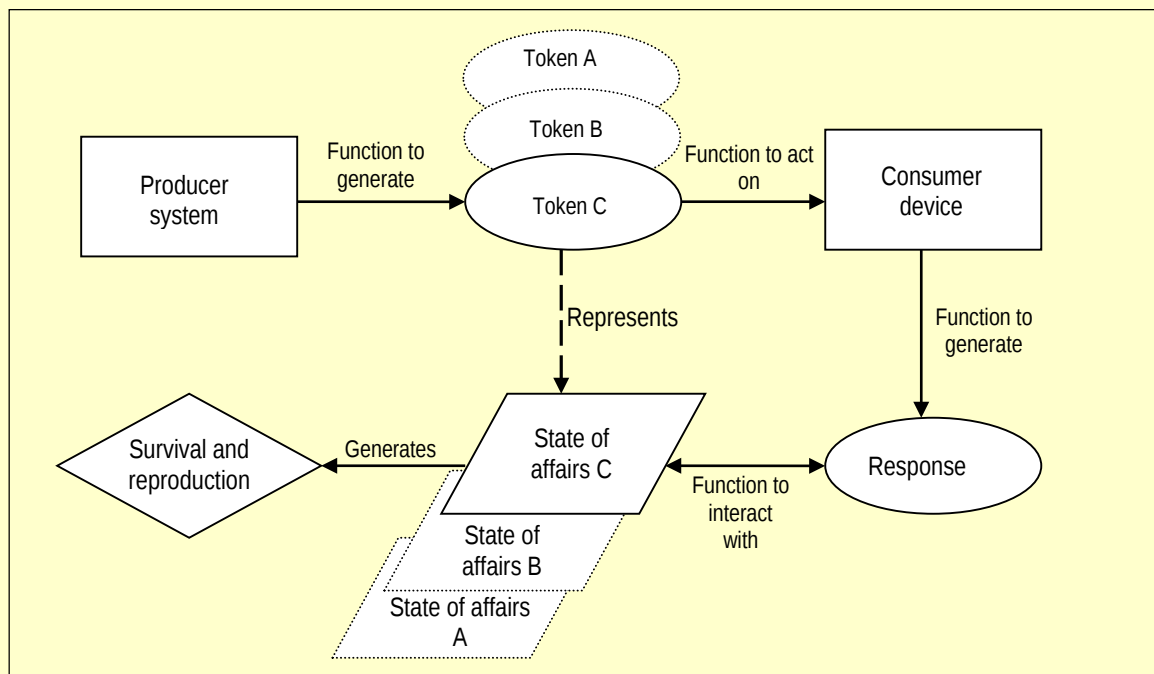
His reason for doing this is to avoid a weakness in representational explanations of behaviour. Broadly, if we explain some successful action of a consumer by reference to a representation and

define the content of the representation by reference to the circumstances in which it prompts successful action by the consumer, our explanation is extremely thin (Godfrey-Smith 1998). Both Millikan and Shea use a requirement that the representational token bears natural information about the state of affairs that it represents to overcome this worry. I discuss this further in section 3.2.8 below.

Fourth, in (c), the evolutionary history of a system is conceived of conventionally as a process in which: genes, or possibly other developmental resources, reproduce in successive generations; they causally contribute to the phenotypes of organisms; their reproduction is imperfect, that is, there is some degree of variation between parent and offspring; variation in reproduction sometimes causes the development of different phenotypes that give affected organisms a greater or smaller chance of surviving and reproducing (higher or lower fitness); so that, over generations, fitness-enhancing mutations become more prevalent in the population of organisms.

Shea's paradigm cases of representational content are illustrated in Figure 7.

Figure 7: The Shea model



It is worth noting again here that what are the functions of a particular system or process is, under an aetiological account of function, an empirical matter. In most real world cases we know relatively little about the selectional history of a particular organ or biochemical process or behavioural trait. So when it comes to identifying examples of representation in the genome, or elsewhere in the biological world, we will need to be a bit tentative. Sometimes it is almost

impossible to believe that the members of a particular reproductively established family do not possess a particular function or that a particular set of items do not possess the kind of functional structure that teleosemantics take to be constitutive of representation. We have to remember, however, that in most cases a measure of doubt remains.

It is also worth repeating here that under this account, a molecular gene may have a number of functions. A phenotypic effect for which a molecular gene was selected gives rise to a biological function for the gene but, depending on the selective history of the gene, it may have a number of such functions. If we think only about representational functions, a single representational type may perform different functions, depending on context. In English, for example, the present tense may pick out an action performed at the time of the utterance ('Now he strikes the shield') or a set of actions spread out over past, present and future ('Lions eat lambs'). At the genomic level, too, a single molecular gene may participate in more than one representational functional structure. Alternative splicing of exons in the expression of molecular genes in eukaryotes (see section 2.2 above) is one means by which a single stretch of DNA may participate in more than one functional structure.

3.2.8 'Infotel semantics'

Shea's model clearly has much in common with Millikan's. The two accounts diverge to some extent in the last step. In both cases, representation requires that it be the function of the consumer device to produce a response to the intentional icon (Shea's 'intermediate') but:

- o according to Millikan, in the case of an imperative icon, that response must map onto the icon; and
- o according to Shea the response must be associated in evolutionary history with states of affairs ('success conditions') in which it has contributed to the success (survival and reproduction) of the ancestors of the consumer device and the representational token must bear natural information about the state of affairs that it represents.

Remember that by mapping, Millikan means

- o the relationship between the icon and the response by the consumer which it is the function of the icon to evoke, follows a mapping rule;
- o according to the mapping rule, a 'critical mass' of icons and states of affairs have entered into correlation patterns;

- o consumer devices have responded systematically to these patterns; and
- o these responses explain their successes, i.e. the responses have contributed to the survival and reproduction of consumer devices.

Millikan's states of affairs in the second dot point above are required to have entered into correlation patterns with past icons of the same family as the icon in question.

Shea's requirement that the representational token bear natural information does not tell us how strong the correlations have to be. Millikan's formulation is preferable because it at least gives us some way of working out how much natural information the token needs to bear, though admittedly the notion of 'critical mass' is not very precise either. It is attractive, though, in that it recognises the possibility that a relatively low level of correlation between the family of tokens and the states of affairs they represent may be sufficient to constitute a critical mass provided the payoff matrix for correctly or incorrectly identifying the target state of affairs is appropriately structured.

3.2.9 Whose success?

Another important feature of teleosemantic accounts of representation, although one that has not attracted a great deal of attention in the literature is the question of just whose success it must be the function of consumer device's response to advance.

Different teleosemantic theories take different approaches to this question, either explicitly or implicitly.

With a purely consumer oriented model like Jablonka's, where the producer of the representational token does not have to be performing any biological function at all, the success which it is the function of the consumption of the token to support can be hardly be anything other than the success of the consumer.

- o The success which it is the function of the consumption of the token to support cannot be the success of the producer device. Black skies cannot be successful or otherwise. They do not survive or reproduce.
- o Nor can it be the success of Jablonka's interpreter device which is taken to be a part of the consumer device (the consumer organism) and so shares its success or failure.
- o It can hardly be the success of the token itself, which is typically some evanescent item like a set of sound waves or a squirt of pheromone or a fleeting bee-dance.

- o Finally, it cannot be the success of the response of the consumer device, because this response is part of a reproductively established family only by virtue of being generated by consumer devices that are themselves part of a lower order reproductively established family.

Shea does not address the question in any particular detail but talks about the success of the ‘representing system’ (2007, p.414). He gives the following examples:

intentional properties are used to explain some kind of success: for the honeybees it is getting nectar, a good for the hive; for the frog it is getting nutritious flying prey; and for the frontal eye fields it is orienting to a location which delivers a reward.

Again, these are all examples where the interests of the producer and consumer devices — the signaling bee and the ‘receiver’ bees, the frog’s fly detection system and the frog’s motor system, the frontal eye fields and the human’s motor systems (or the human as a whole) — are in close, if not perfect alignment.

Millikan also focuses on cases where the producer has the relational proper function of eliciting a response from the consumer and the consumer has the relational proper function of responding to the token generated by the producer.

It is true that in many cases success for the producer entails success for the consumer and vice versa and, in particular, that in many sub-organismal cases the producer and consumer devices share the same fate, so that success for one is success for the other. For example, the DNA that acts as a template for the synthesis of an mRNA and the ribosome that synthesizes the enzyme in accordance with the sequence of nucleotides along the mRNA are part of the same cell and share its fate: if it dies, they do not survive and reproduce. Similarly, the gland that produces the hormone and the cells that react to its presence by multiplying more rapidly (or whatever it happens to be) are part of the same organism: they can survive and be reproduced only if it does.

Exactly whose success must be supported by the performance of which function is of little significance in cases where the survival-and-reproduction interests of the producer and consumer devices are aligned but can make a significant difference in cases where those interests diverge. For example, if we hold that a token represents a state of affairs only if it is the function of the consumer device to respond to the token in such a way as to support the success of the consumer device in the presence of the state of affairs, then we have problems dealing with instances of deception, where it is not the function of the consumer device to respond to the token so as to support the success of the consumer device in the presence of the state of affairs that the token would naturally be taken as representing.

I think we have to say that a token represents a state of affairs if, provided that the consumer device performs its function properly, the consumer's response to the token supports its survival and reproduction. This allows for cases where the consumer device is 'deceived' by a token generated by the producer device and also allows us to distinguish between deception (where it is the function of the deceptive producer to cause the consumer not to perform its function properly) and miscommunication (where the two functions are adapted to one another but where, for one reason or another, either the producer or the consumer fails to perform its function).

In most of the cases considered in this essay, there is a complete, or close to complete community of interest between the producer and consumer — they are part of the same organism and share the same evolutionary fate — so that the answer to the question 'whose success' makes no difference. But it is an issue of much more significance for a general theory of representational systems which must be able to deal effectively with cases where the interests of producer and consumer overlap only partially, if at all.

3.2.10 What has the content?

I think it is worth noting, in passing, that the literature on teleosemantic theories of representational content is not entirely consistent in its view about what exactly it is that possesses representational content. Is it:

- o the token produced by the producer; or
- o the producer device; or
- o the system constituted by the token and its reception (or interpretation) by the consumer device?

Majority opinion in the literature seems to be that it is the token produced by the producer device that possesses representational content. So, for example, Shea says, 'a representation's content — the message or instruction it carries — is a property of the representational token (the sentence, signal or pattern of neural firing).' Braddon-Mitchell and Jackson (1997) distinguish 'contentful states' from the mechanisms that produce the states, as does Neander (1995). MacLaurin (2008) speaks about attributing content to thoughts, rather than their producers and consumers.

This seems consistent with normal usage in relation to paradigmatic representational systems like natural language. It seems more natural to say that an utterance has representational content than that the hearer does (although we would naturally say that the thoughts of a human hearer also have representational content).

Other writers — e.g. Beckermann (1988) — prefer to ascribe content to the whole system that produces and consumes representational tokens, that is, the system that consists of producer, token and consumer.

Jablonka (2002) seems to think that the producer device bears representational content: ‘A source [what I call a ‘producer device’] can be said to have information when a receiver system [what I call a ‘consumer device’] reacts to this source in a special way.’ Later in the same article, however, she talks about ‘a reaction’ (by the consumer device) being ‘informational’.

Of course, under a teleosemantic approach the token has to be produced in the right way by a producer device with the right kind of functions, so perhaps in the end not all that much hangs on this question. At least, if:

- o two accounts conclude that exactly the same set of consumer-token-producer processes generates representational content;
- o the coincidence of the sets is counterfactually robust; and
- o each account attributes the same content to each consumer-token-producer process; then

each account agrees on attributions of representational content in the actual world and across possible worlds as well, so it seems merely a matter of convenience whether we attribute content to the producer or the token produced, or the process of production, for that matter.

3.2.11 Conclusions about the different teleosemantic accounts (and how much the differences matter)

I think Millikan’s teleosemantic framework, as set out primarily in *Language, Thought and Other Biological Categories* (1984), is as good an account as any so far formulated.

In this essay, I will primarily use her account to assess the representational features of various genomic processes but I will refer to the accounts of Shea and Price when they lead to different conclusions about the existence of representational content in a particular case or about what that content is. This will not happen very often.

Under all three approaches, we will find that the expression of molecular genes can, at least sometimes, represent particular cellular conditions. Whichever formulation we choose, those conditions will be determined by the selective history of the molecular gene in question — i.e. if the molecular gene has been selected for its capacity to act as a template for the synthesis of a

protein that helps the cell, or containing organism, deal with particular cellular conditions, then the expression of that gene represents those conditions.

There will sometimes be divergences. For example, Shea's account requires that the content of a representational token can only be evolutionary success conditions, while Millikan's slightly more elastic account allows a wider range of possible contents. As a consequence, under Shea's account, a molecular gene cannot represent the protein for whose synthesis it customarily acts as a template, while under Millikan's account, it can.

The differences between the accounts, then, are not trivial but my overall approach to them is basically pluralist. The accounts put forward by Millikan, Shea and Price are all plausible attempts to characterise representation from a teleosemantic starting point. The differences between them are *relatively* minor and I am not sure there is much to be gained by spending a long time arguing over which one best captures 'true' representation. We can find out just as much about representation in the genome if we talk about Millikan-representation, Shea-representation and Price-representation — rather than picking one of them — so long as we are clear about the differences between them and, particularly, clear about the circumstances in which they give different answers to the question whether a particular process (or token) constitutes representation or the question of what the representational content of a process (or token) is.

3.3 Challenges to teleosemantic accounts

I have set out what I see as the most convincing teleosemantic account of representation but in doing so I have not sought to defend this particular account, or teleosemantic accounts more generally, against all the objections that have been brought against them. I am relatively optimistic that most if not all of these objections can be adequately met but to explore them all would occupy another essay of this length and is not feasible in this context. Still, I think it is important to acknowledge the most important objections.

- o *Indeterminacy.* Many people believe that the notion of biological function is insufficiently fine grained to underpin a semantics for natural language or for human thought. The standard example is the frog's tongue striking at a passing fly.' the frog sees the fly, neurons fire in its head and its tongue flicks out towards the fly. What is the content of the neuronal firings: 'there's a fly' or 'there's some food' or 'there's a little, moving black dot' or 'there's a little black, moving bit of food'?

- o *Swampman*. The idea here is that the content of a representational token cannot depend on the evolutionary history of the systems that generate it but must depend on how the token and the systems associated with it work now (see contributions from Papineau (1984); Millikan (1996)). A ‘swampman’ who is physically just like a human but who comes together through some cosmic fluke looks like a human and behaves like a human and speaks like a human but his words and neuronal patterns lack the right evolutionary history to give them representational content on a teleosemantic view. This is a problem for all teleosemantic accounts of representation, not particularly for accounts of genetic representation. (My favoured response is just to bite the bullet and say that swampman’s words and neuronal patterns do not bear representational content, just as we would deny that an inscription of the sentence ‘Pericles was an Athenian’ is about Pericles if it is made up of seed pods on a beach that have been blown into the pattern of the letters by the wind.)

- o *Novel content*. Obviously in more sophisticated representational systems like natural languages, particular tokens can bear determinate novel content: content that no token previously produced has ever borne. But if content is determined by the token’s function and if that function is determined by what the producer or consumer devices have been selected for, it is at least not clear how a token could have entirely new content that has played no part in the selective history of the producer or consumer devices. This is more of an issue for teleosemantic accounts of sophisticated representational systems like natural languages than for relatively simple systems like the genetic systems we are considering in this essay. In the genetic case, the representational content of a token is derived in a relatively direct way from the evolutionary history of the systems that produce and consume it. Even in more sophisticated systems, though, the problem does not seem insuperable. Let us take as an example a novel utterance like ‘the tiger that my niece Arsinoë teased has died’. The different tokens that combine in this expression need not be thought of as performing *direct* proper functions in this context. We might think that ‘Arsinoë’ has the direct proper function of picking out my niece but clearly the reproductively established family of the word ‘tiger’, of which the ‘tiger’ token in my utterance is a member, does not have the function of picking out a particular tiger. Instead, it has a number of adapted functions, to combine with various other classes of words to pick out different tigers or sets of tigers. As Millikan puts it (1997, p.94):

what natural selection selected [in the case of mental representations] was a very complex system designed to interact with the environment in the development of

concepts, methods of concept formation, the fixing of beliefs, and their use in theoretical and practical inference, ultimately producing adapted behaviors.

- o *The epistemological objection.* The idea is that people — normal people, non-philosophers or ‘the folk’ — have today (and have for many thousand of years past, had) justified true beliefs about the content of other people’s intentional states (which states possess representational content). But in the huge majority of cases they have not had justified true beliefs — or any beliefs at all — about the selectional history of the mechanisms that have generated those states. So having an intentional state with such and such content is not identical with being in a state with a particular selectional history (Jackson 2006). Again, this is more a problem for teleosemantic accounts of human beliefs and desires than for accounts of representation in the genome. (I am not sure how to meet this but a lot seems to hang on the notion of identity. My intuition is that a person can have a justified true belief about some kind of entity without having access to the best available philosophical or scientific account of that kind of entity.)
- o *Function now and function then.* Developmental resources like molecular genes only have selectional properties if they are closely enough associated with heritable phenotypes. A molecular gene must have correlated with its selectional properties at the time it was selected but it may not have done so in the recent past, in which case it may no longer be predictive of its selectional properties. It may, for example, have become causally necessary for many different phenotypes and be predictive of none of them in particular. Of course, a core process that has become generatively entrenched may retain its functions pretty much permanently: they are essential to the development of the organism so that mutations that disturb the process are overwhelmingly likely to be badly maladaptive (Wimsatt 2001). How much biological functions have faded over time is an empirical question, and one which it will surely be very difficult to answer in many cases, but it is an important constraint on any teleosemantic theory of representation in the genome.
- o *Not enough selection.* Even if we accept a teleosemantic account of representation by nucleic acid structures, it is an empirical question just how many nucleic acid structures bear representational content and how significant that content is in evolutionary biology. In particular, if a nucleic acid structure acts as a template for the production of a certain polypeptide, but has not been selected to do so, then on a teleosemantic account, it lacks the biological function of producing that polypeptide and so cannot represent it, or any of its downstream effects. If it turns out that natural selection is relatively unimportant in

sustaining reproductive families of nucleic acid structures, then we might be obliged to conclude that very few nucleic acid structures bear representational content. So, for example, if it turns out that random drift plays a pervasive role in the persistence and disappearance of families of nucleic acid structures, we may be obliged to conclude that there is very little representational content among nucleic acid structures. My feeling is that this will probably not turn out to be a very strong objection. In many cases, the representations generated within a cell that allow it to respond successfully to changing circumstances both within and outside its borders are so fundamental to the maintenance of all cellular biota that it is hard to imagine that mutations in these mechanisms are not weeded out by ‘purifying selection’ in the normal course of biological events.

- o *Too parochial.* It could also be argued that teleosemantics offers nothing more than a biological account of representation as it has occurred here on earth, while what we really want is an conceptual account of representation that tells us how to recognise representation wherever and whenever it might arise. In other words, it might be claimed that a teleosemantic account of representation is too parochial. This is a deep though, I believe, a misguided criticism. Take a concept *X*. One philosopher says, ‘*X* means *A* or (*B* but not *C*)’. Another philosopher says, ‘But we can imagine a possible world with flying pigs and a different Planck’s constant where a thing could be *B* but not *C* but also *Y* and *Z* and we surely do not want to say that something that is *Y* and *Z* is *X*; that would be terribly counterintuitive.’ The problem with this kind of argument is that we do not know what sort of a world that would be: what structures could be left unchanged, what laws could persist and which ones would have to be different. Wittgenstein said the world is the totality of facts not of things (1922, §1.1) and it is perhaps tempting to think that you can sensibly discuss possible worlds by deleting a few of the denumerably many sentences that constitute the totality of facts about this world and inserting a few others. But I do not think you can. We do not understand enough about the structure of *this* world to talk sensibly about these bizarre and remote possible worlds. I think the proper response is to say that when we come across a world — or a bit of this world — with flying pigs and a different Planck’s constant, we will investigate it and try to build a theory to describe it but that, until we do, it is neither possible to build such a theory nor fruitful to try. So I do not think this parochialism objection is a good one.

This is quite an impressive catalogue of objections but, apart from the comments on them made above, I will not deal with them in this essay.

4 Three kinds of genomic representation

Given this teleosemantic view of representation, I believe that nucleic acid structures, particularly the mRNAs produced in the course of gene expression, do bear representational content. Later in this section I will consider what kind of things nucleic acid structures might represent but it may be useful first to say something about how these representational capacities fit into the range of representation we find around us today and the way it is reasonable to suppose that representation has evolved in different biological contexts over time.

As I suggested in section 1.1, teleosemantic representation arises in a whole set of biological contexts.

- (1) The most basic and oldest are the cellular processes, driven by the genome, that I am exploring in this essay.
- (2) Symbiotic relationships between different species also involve the coordination of activities in response to conditions in the external environment or, very often, in the internal environment of the host organism.
- (3) Swarms of unicellular organisms, which we would not regard as a single organism are also able to coordinate their activities and adapt their coordinated behaviour to the environmental circumstances (Shapiro 2007).
- (4) Among metazoans a host of finely tuned regulatory systems coordinate the way in which their component systems coordinate their activities to meet the demands of the internal or, more indirectly, the external environment. In mammals, for example, hormones coordinate chemical activity in different parts of the body to control growth, to activate or inhibit the immune system, regulate the metabolism, initiate and control developmental phases like puberty and parenting, and regulate the reproductive cycle.
- (5) Coordination of activities between individuals of the same metazoan species ranges from simple warning cries to more complicated systems like the bees' waggle dance and finally human natural languages.

In the list above I have identified five biological contexts in which we find representation on the basis of the size and complexity of the biological entities that participate in them but it seems

likely that the order of the items in the list also reflects the order in which these kinds of representation arose.¹²

Maynard Smith and Szathmáry (1995, p.6) identify five major transitions in the history of life on the grounds that ‘entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it.’ Three of the five — the appearance of chromosomes, the development of eukaryotes, and the origin of sex — happened before the appearance of multicellular organisms.

Of course it is hard to be sure about events so far in the evolutionary past, but it is possible to imagine that the normal processes of mutation and natural selection could at a very remote time have given rise to coordination of activities between different kinds of simple replicators that assisted their survival and reproduction. Similarly, the emergence of cell membranes and metabolism early in the history of life, must have involved trade-offs in the allocation of energy resources between metabolism, replication and maintenance of the cell membrane (Hartwell, Hood et al. 2000, p.787). Eukaryotic cells themselves are thought to be the product of symbiotic relationships between earlier independent lineages (Ridley 2000, p.135).

In many cases like these, the costs and benefits of signaling — in terms of the likelihood of survival and reproduction — are such that the evolution of biological systems that produce signals with the function of adapting consumer systems to the environment seems almost assured. The details go beyond the scope of this essay, but evolutionary game theory provides a powerful theoretical tool for predicting what kind of representational systems are likely to emerge, given the populations of consumers and receivers, the costs and benefits of producing signals and the costs and benefits of receiving and acting on them (Skyrms 2010).

So I will be arguing that representation in the genome is both the most basic kind of biological representation we find today but also the kind that evolved earliest in the history of life. It comes first in a long line of representational systems that solve biological coordination problems and so contribute to the fitness of the entities that participate in them.

¹² We would certainly want to put symbiotic relationships second rather than, say, fourth if we subscribe to the widely held theory that some of the organelles of eukaryotic cells are the evolutionary product of an increasingly intimate symbiotic relationship between different lineages of prokaryotic organisms.

Just as researchers are now developing general theories of the evolution of cooperation (Axelrod and Hamilton 1981, and a large literature since), we are also moving towards a general theory of signaling and coordination that aims to explain:

- o when and how signaling (and eventually representation) emerges in response to coordination problems;
- o what kind of overlap of interest between the participating systems is necessary;
- o what error rates are tolerable;
- o what the costs and benefits to producers and consumers must look like, etc.

In section 9.4 I will argue that a teleosemantic theory of genomic representation both constrains and benefits from, general models of this kind.

So, now, what sort of representational content might genome level phenomena, the nucleic acid structures, bear?

4.1 Representing proteins

An obvious candidate for a genome-based representational system is the ‘genetic code’ that links base triplets along a strand of DNA with particular amino acids in a synthesised protein. So, for example, if a cytosine-guanine-cytosine (CGC) triplet on a DNA strand is expressed through the transcription-translation process outlined in section 2.2 above, it will always give rise to an arginine molecule in the final protein constructed at the ribosome.

Since there are four kinds of nucleotide along a strand of DNA, there are 4^3 , or 64, possible base triplets. Each of these corresponds to one of the twenty amino acids that figure in the proteins that occur in all living things, or in three cases, brings the transcription process to an end.

The first elements of this code were discovered by Nirenberg, Ochoa and others in the 1960s and its final elements established in 1967 (Kay 2000). Each codon can act as a template for the synthesis of at most one amino acid but nearly every amino acid has more than one codon that can act as a template for its synthesis.

Table 1 sets out the genetic code that obtains in the huge majority of organisms that have been investigated, except in mitochondrial DNA (see section 6.3 below). By convention, the codons

are described as they occur in mRNA (where uracyl appears) rather than DNA (where thymine appears).

Table 1: The genetic code

	U		C		A		G		
U	UUU	Phenylalanine	UCU	Serine	UAU	Tyrosine	UGU	Cysteine	U
	UUC		UCC		UAC		UGC		C
	UUA	Leucine	UCA		UAA	Stop	UGA	Stop	A
	UUG		UCG		UAG	Stop	UGG	Tryptophan	G
C	CUU	Leucine	CCU	Proline	CAU	Histidine	CGU	Arginine	U
	CUC		CCC		CAC		CGC		C
	CUA		CCA		CAA	Glutamine	CGA		A
	CUG		CCG		CAG		CGG		G
A	AUU	Isoleucine	ACU	Threonine	AAU	Asparagine	AGU	Serine	U
	AUC		ACC		AAC		AGC		C
	AUA		ACA		AAA	Lysine	AGA	Arginine	A
	AUG	Methionine (start)	ACG		AAG		AGU		G
G	GUU	Valine	GCU	Alanine	GAU	Aspartic acid	GGU	Glycine	U
	GUC		GCC		GAC		GGC		C
	GUA		GCA		GAA	Glutamic acid	GGA		A
	GUG		GCG		GAG		GGG		G

It is enormously attractive to regard this genetic code as a representational system. Stretches of DNA that act as templates for the synthesis of particular proteins look as though they could represent that protein. After all, the protein is very different from the stretch of DNA but is related to it through a straightforward algorithmic code — although there *are* sometimes plenty of causal twists and turns between DNA and protein (see section 2.2 above). Surely, in some intuitive sense, the codons along the DNA strand stand for the amino acids in the polypeptide chain to which they correspond.

Moreover, it is tempting to think that evolution and inheritance use DNA as a stand-in for the protein: proteins are not replicated directly, from one protein molecule to another, but indirectly through the DNA-RNA mechanism. It looks (at least) as though the function of DNA codons in the genome is to stand for the amino acids for whose synthesis they act as a template.

4.1.1 mRNA as a Millikan intentional icon

While our intuitions that the genetic code constitutes a representational system may be strong, the kind of teleosemantic account that we are working with in this essay requires a particular functional structure before we can recognise a representational system and representational

content. In particular, we need to identify appropriate producers, tokens and consumers in the context of protein synthesis. Suppose we take: a coding region of DNA, RNA polymerase and the spliceosome as the producer device; an mRNA as the candidate intentional icon; and the ribosome and tRNAs as the consumer device.

Let's start with Millikan's characterisation of an intentional icon. According to her, if an mRNA is to be an intentional icon it must fulfill three basic conditions:

- (1) The mRNA must be a member of a reproductively established family with direct proper functions.
- (2) Normally, the mRNA must mediate between a producer device (a coding region of DNA, RNA polymerase and the spliceosome) and a consumer device (the ribosome and tRNAs), the presence and proper functioning of each being a Normal condition for the proper functioning of the other.
- (3) Normally, the mRNA must adapt the ribosome to conditions in such a way that it can translate the mRNA into a protein.

Whether the icon is imperative or indicative or both at once ('pushmi-pullyu') we will discuss below.

In relation to (1), mRNAs are clearly members of reproductively established families, and they possess at least the direct proper function of acting as the proximate template for protein synthesis at the ribosome. I am not sure that any further argument for this proposition is needed but perhaps it would be useful to note that mRNAs are essential for the synthesis of the proteins that constitute the fabric of, and catalyse the reactions that build and maintain, all living cells. Our knowledge of the ancient processes by which mRNA came to acquire its current role in cell biology is partial and speculative, but it seems quite implausible to claim that this ubiquitous and crucial role in the maintenance and reproduction of living things is not a bona fide biological function. So I think we can take it that (1) is satisfied.

In relation to (2), it seems fair to say that Normally — that is, in the range of circumstances that have accounted for the survival and reproduction of the mRNAs ancestors — mRNA mediates between the producer and consumer devices described above. The function of coding regions of DNA is to act as a template for protein synthesis in particular circumstances. They cannot perform this function if the consumer device, the ribosome, does not perform its function of synthesising and stringing together the amino acids that form the protein. Similarly, the tRNAs

and ribosome cannot perform their function without the DNA to act as a template for the production of the mRNAs. So (2) is satisfied.

In relation to (3), the mRNAs cause the consumer device, the ribosome and the tRNAs, to perform its function, translating the mRNA into a protein, by initiating translation. For example, in prokaryotes translation begins at a 'ribosome binding site' on the mRNA defined by a specific short sequence of nucleotides (the 'Shine-Dalgarno sequence') adjacent to an AUG 'Start' codon. A specialised tRNA whose anticodon is complementary to AUG carries a modified methionine molecule (known as an 'fMet') whose amino end is blocked by a formyl group. This tRNA can function only at a binding site; an AUG codon within the reading frame is translated by a tRNA with an unmodified methionine. During initiation, a particular ribosomal RNA ('rRNA') binds to the Shine-Dalgarno sequence and the fMet tRNA binds to the mRNA's initiation codon. 'Elongation factors' then facilitate sequential translation of mRNA codons to amino acid acids in the growing protein. The process in eukaryotes varies in relatively minor ways.

Millikan's formulation makes it sound as though there has to be a couple of distinct processes going on: first the intentional icon adapts the consumer device, then the consumer device performs its functions but it seems moot here whether we discern two different processes — the adaptation of the consumer device and its performance of its function — or just one.

We could say that the initiation phase of translation, leading up to the translation of the first mRNA codon, constitutes the adaptation of the consumer and that the actual translation of the codons constitutes the performance of the function. Or, at a less detailed level of description, we could say that there is only one process going on — the synthesis at the ribosome of the protein for which the mRNA acts as a template — and that this constitutes both an adaptation by the mRNA of the consumer device (the ribosome etc) and the consumer device's performance of its function.

Whichever way we go, it is plain that it is the appearance of the mRNA at the ribosome that prompts the initiation of translation, so that the mRNA is adapting the consumer device (the ribosome etc) to the conditions that prompted transcription back in the nucleus. So I think we can take it that (3) is satisfied.

Millikan distinguishes between two fundamental kinds of intentional icons, imperative and indicative. She characterises them in the following way:

- (4) If the mRNA is an imperative intentional icon, it must be the proper function of the ribosome to respond to the mRNA by producing a protein onto which the mRNA will map.

- (5) If the mRNA is an indicative intentional icon, the Normal explanation of how the mRNA adapts the ribosome so that it can perform its proper function must refer to the fact that the mRNA maps onto something else'. In other words, it is the function of the consumer to respond to the icon in some particular way and it cannot do this, at least not Normally, unless the icon maps onto something else.

Should we see codons in DNA as imperative or indicative icons?

It is perhaps more tempting to see the mRNA as an imperative icon: that is, to think that it is the proper function of the ribosome etc. to respond to the mRNA by producing a protein onto which the mRNA will map. The protein generated at the ribosome is meant to correspond to the final RNA from which it is translated and the genetic code constitutes the mapping rule.

Alternatively, we could take mRNAs to have indicative content. If so, according to Millikan, 'the Normal explanation of how the mRNA adapts the ribosome so that it can perform its proper function must refer to the fact that the mRNA maps onto something else'. That something else could be the 'sense' DNA strand from which the mRNA has been transcribed. The Normal explanation of how the mRNA adapts the ribosome etc so that it can perform its proper function refers to the fact that the mRNA maps onto the sense strand. In this case, the mRNA is a pushmi-pullyu representational token which at once bears indicative representational content — the arrangement of the sense strand — and imperative representational content — the arrangement of the amino acids in the synthesised protein.

We could perhaps see the 'something else' as the activity of the regulatory elements that turn on the molecular gene, for it is only when molecular genes are expressed at the right time that protein synthesis has its typical adaptive role. Indeed many diseases arise from malfunctions in the regulation of gene expression that cause too much or too little of a protein to be synthesised. For example, among many other examples, malfunctions in gene expression have been implicated in cancer (Gray and Collins 2000), Alzheimer's disease (de la Monte and Wands 2005) and schizophrenia (Harrison and Weinberger 2005). If we take this view, though, we must conclude that the mRNA is representing the conditions associated with the activity of the regulatory system. This is a plausible claim, which we will explore in detail in section 4.3, but it does not establish any representational relationship between the mRNAs and either the protein for whose synthesis it acts as a template or the DNA from which it is transcribed.

As we have seen in section 3.2, Millikan also identifies a particular, primitive form of icon which is neither imperative nor indicative but both at once, or 'pushmi-pullyu' in Millikan's terms. The function of a pushmi-pullyu representation is 'to mediate the production of a certain kind of

behaviour such that it varies as a direct function of a certain variation in the environment, thus directly translating the shape of the environment into the shape of a certain kind of conforming action' (Millikan 1995, p.190)

In the case of transcription and translation, the mRNA transmits an instruction to the ribosome (and associated machinery) with content something like 'build a protein with such and such successive amino acids'. But remember that, on Millikan's account, an indicative icon (the mRNA in this case) affects its consumer device in a way that allows the consumer to perform its function only if certain conditions hold, in this case, if the mRNA reflects the DNA from which it has been transcribed. So mRNA in this case has both imperative and indicative content. Moreover, the behaviour of the translational apparatus at the ribosome varies as a direct function of the DNA pattern reflected in the mRNA, thus reflecting the shape of the DNA environment into the shape of the ribosome's conforming action. In light of this we may be better off regarding mRNA as a pushmi-pullyu representational token rather than either an imperative or an indicative token.

4.1.2 Shea representation

It is important that Shea's more demanding model of representation rules out the genetic code as a genuinely representational system.

The core of the difficulty is that Shea's model is essentially a model of communication between producer and consumer that conveys information about the environment *by adapting the activity of the consumer to the environment*. Even if we think of the environment broadly, as including chemical conditions within the organism or the particular cell, it is hard to see how the transcription-translation processes of gene expression adapt the consumer device (the ribosome etc.) to the environment.

Remember that, according to Shea (2007, p.419), *mutatis mutandis*:

An mRNA of type R has content C if:

- (a) R-type mRNAs are intermediate in a system consisting of a producer (DNA, RNA polymerase, the spliceosome etc) and a consumer (tRNAs, the ribosome) cooperating by means of a range of mediating representations (the range of RNAs) — all specified non-intentionally — in which every representation in the range also satisfies (a) to (d);
- (b) R-type mRNAs carry the natural information that C obtains;

(c) an evolutionary explanation of the current existence of the producer-intermediate-consumer system adverts to R-type mRNAs having carried information about C; and

(d) C is the evolutionary success condition, specific to R-type mRNAs, of the behaviour of the tRNAs and ribosome system prompted by R-type mRNAs.

The first three elements of Shea's formulation seem to be satisfied in this case.

- o Paragraph (a) causes no problem. It certainly seems that the first two parts of (a) are satisfied in the case of protein synthesis. First, the producer and consumer devices, defined as above, do cooperate by means of a range of mediating tokens, the mRNAs (and it is their function to do so). Second, all three elements of the system are specified non-intentionally. Of course the third requirement — that every token in the range satisfies (a) to (d) — remains undecided at this point.
- o Consistent with the idea that mRNAs are pushmi-pullyu representational tokens, we can find two kinds of natural information that is carried by R-type mRNAs: that a particular protein will be synthesised at the ribosome (corresponding to Millikan's imperative content) and that the mRNA reflects the DNA from which it has been derived (corresponding to Millikan's indicative content). Naturally neither content may be right: the mRNA may not make it to the ribosome or there may have been a transcriptional error in the processing of the mRNA, but natural information is never 100 per cent reliable. Smoke still bears natural information about fire even though smoke sometimes arises in the absence of fire.
- o Paragraph (c) is also satisfied. It seems overwhelmingly likely that an evolutionary explanation of the producer-intermediate-consumer system adverts to R-type mRNAs having carried natural information about the fact that the relevant protein will be synthesised at the ribosome.

It is when we get to paragraph (d) that we run into trouble. In defining evolutionary success conditions, Shea (2007, p.416) says:

Recall that, for teleosemantics, success conditions are also constitutive of content, where success is survival and reproduction of the representing system. A representation R has the content C because, in the past, R caused a consumer subsystem to behave in a way that contributed systematically to survival and reproduction iff R truly represented that C.

In the protein synthesis case the putative content C — that the relevant protein will be synthesised — is identical to the behaviour of the consumer device that has contributed to the

survival and reproduction of the representational system. But for Shea, representation only arises when the representational token adapts the behaviour of the consumer device to its C. That cannot happen in this case because no token can adapt the behaviour of the consumer device to the behaviour itself.

We have to conclude that Shea's account of minimal representation doesn't work for protein synthesis. I will argue in section 4.3 that on Shea's account an mRNA token can represent environmental conditions in which synthesis of a particular protein has contributed to the survival and reproduction of the representational system but we cannot plausibly argue that an mRNA token represents the behaviour of the consumer device that it is its function to cause.

4.1.3 Causal wrinkles do not compromise representational content

The biological background set out in section 2 makes it clear that the causal relationship between the sequence of nucleotides in the DNA of an organism's cells and the proteins that are synthesised at the ribosomes of those cells is a complicated one. In particular:

- o very few of the coding regions on the DNA in an individual cell actually act as the template for the synthesis of a protein; and
- o alternative splicing of exons can create different mature mRNAs and hence different proteins after translation.

We should note here that the ambiguity introduced by alternative reading frames and alternative splicing — see section 2.2 above — means that a single DNA sequence may represent more than one protein, but it does not mean that the sequence, read in a particular direction from a particular starting point, fails to represent at all. Of course it may very easily fail to do so because it has no biological function or because its function is not representational in a teleosemantic sense. Indeed, most RNA sequences — our representational tokens — fail to represent for one of these two reasons. But the fact that the function of the sequence is to act as the template for the synthesis of a protein only when read in one direction from a particular starting point does not mean it does not represent. We might compare a fragmentary inscription in an ancient language where word boundaries are not indicated. The content of this inscription is successfully communicated only when it is read from a particular point, and only where successive word boundaries are correctly inferred, but it is still a representational token.

This sort of complexity detracts from the clean lines of the DNA 'code'. If DNA acted very directly as a template for the production of proteins, so that every protein produced in a cell was composed of a string of amino acids, each of which corresponded directly to consecutive codons

in the DNA, our intuitions might be stronger that the DNA coding regions bear representational content concerning the relevant proteins. The more bells and whistles we add to the story, the less compelling seems the semantic claim.

Yet the fact that the process by which DNA sequences are transformed into amino acids and proteins is a complex one is not sufficient to establish that DNA do not represent the acids or proteins. There are plenty of very complicated codes — the Enigma machine, codes based on code books, steganography or combinations of these — that must surely be representational systems.

Similarly, the causal complexity of the DNA-protein relationship does not mean that the DNA cannot bear representational content concerning the protein.

Compare

(1) CLAP*YOUR*HANDS

with

(2) PERFORM*THE*INSTRUCTION*DERIVED*BY*OMITTING*ALL*THE*ODD-NUMBERED*CHARACTERS*FROM*THE*STRING*‘ECGLSAFPM*KY*OXUARQ*MHDAENJDLS’

You have to do a bit more work with the second sentence than with the first before you start clapping, but the combination of the second-level instruction about removing the odd-numbered characters and the first-level string between the inverted commas is no more ambiguous than (1). Indeed a degree of causal complexity is surely necessary for more sophisticated representational systems that are capable of performing complicated inferences based on a clear separation between indicative and imperative icons.

4.1.4 Being clear about ‘translation’

What follows may be pretty obvious but before we move on I think it is worth being quite clear that — even if we think that mRNAs represent the proteins for whose synthesis it is their function to act as a template — there are two fundamental differences between translation from mRNA to protein and translation from one natural language to another.

First, translation in the genetic sense is a feature of just one representational system. That’s obviously different from the case of natural languages where translation arises when a token of one representational system is transformed into a token of another.

A particular type of mRNA represents a particular protein in part because it is the function of the mRNA to be ‘translated’ into the protein at the ribosome. But there is only one representational system involved. The genetic code is not a way of transforming tokens in one representational system into another.

Second, in the case of the genetic code, representation only works in one direction. Nature builds proteins on a template contained in a cell’s DNA but doesn’t build DNA on a pattern contained in a protein.

It is the ‘central dogma of molecular biology’ (Crick 1970) that DNA or RNA may act as a template for proteins but proteins cannot act as a template for DNA or RNA. That is, ‘information’ (of some kind or another) can flow from DNA or RNA to protein, but not vice versa. So if DNA (or some other genetic structure) does semantically represent proteins, or phenotypes, or anything else causally downstream from the proteins, it is representing items that do not themselves represent. If the central dogma is right, the protein synthesis representational system displays the same directional asymmetry as natural languages. The word ‘dog’, at least in some utterances, represents dogs — a particular dog or a particular set of dogs or all dogs — but no dog represents the word ‘dog’.¹³

In this the genetic code differs from a code in any everyday sense, where a code is a means of transforming a plaintext character string into a ciphertext string which can be transformed back into the plaintext string by a recipient armed with the right information (Wrixon 1998, p.131). In other words, the original token is transformed into a token in a different representational system and can be transformed back into the original.

4.1.5 Conclusions

If we are trying to identify a representational system related to the genome, the genetic code is the most obvious candidate. The correspondence between the codons on a stretch of DNA and the amino acids in the protein for whose synthesis the DNA acts as a template simply *looks* like a

¹³ Note though, that if we think that DNA represents mRNA, and mRNA represents proteins, we do have a situation where one representational system is transformed into another. It should also be noted that, while the curious behaviour of prions and ‘a few retro-copying phenomena accepted on all sides’ (Griffiths 2001, 407), may pose a threat to the absolute status of the central dogma, they do not undermine the idea that genes – stretches of DNA – contain semantic information about amino acids, proteins or phenotypes. At most they suggest that if DNA conveys semantic information, other molecular structures may do as well.

representational system. But when we examine the transcription-translation process carefully, against the main teleosemantic models, we find that matters are not as clear as we might have thought. It is possible to see mRNAs as intentional icons under Millikan's account, and therefore as bearers of (rudimentary) representational content. But if we use a slightly more demanding account like Shea's — which requires that the representational token adapt the behaviour of the consumer device to the environment — we find that neither coding regions of DNA nor the mRNAs transcribed from them bear representational content.

This is an interesting, perhaps surprising, result. It brings into sharp focus the powerful emphasis on consumer-producer dynamics that characterises teleosemantic approaches to representation. The genetic code has plenty of features that make it look like a (formal) language: its compositionality, its digital nature, and the flexibility in the arrangements of amino acids in whose synthesis it participates. These are important similarities, but under Shea's model we must conclude that neither DNA coding sequences nor the mRNAs derived from them represent the proteins for whose synthesis they act as a template.

4.2 Representing phenotypes

In the classes of cases considered so far, we have seen DNA, in combination with other nucleic acid machinery, generating mRNA tokens that represent the proteins for whose synthesis they act as a template.

I have argued that on Millikan's account of intentional icons, these tokens display a kind of basic pushmi-pullyu representation at a genetic level but that, under Shea's more demanding account of representation, which identifies the content of a representational token with the its evolutionary success conditions, it is not possible to discern representation in the process of protein synthesis.

However, it is clear that many biologists mean more by talk of genetic representation than the coding relationship between DNA sequences and the proteins for whose synthesis they can act as a template. Descriptions of the genome as a 'blueprint' or 'instructions' for the making of an organism strongly suggest that particular parts, or sets of parts, of the genome represent particular traits.

To take just a couple of examples, in an influential article from 1997, Szathmary and Smith say:

Existing organisms ... do not reproduce by copying. Instead, they contain DNA that is copied, and that acts as a set of instructions for the development of the organism. (Szathmary and Smith 1997, p.556)

And in a later essay (2006) on the genetics of the nematode *Caenorhabditis elegans*, Thomas Bürglin makes no bones about his view that ‘the information required to make a complete organism is contained within the genes of the genome’:

the gene products — that is, the proteins — can and do react to environmental influences but ... each reaction ... is a direct consequence of the protein sequence which in turn is derived from the gene sequence.

It is clear enough here that the molecular genes are thought of as containing information about the phenotype of the adult organism — not just about the proteins for whose synthesis they customarily act as a template.¹⁴

Monogenic traits instantiate the simplest and most direct causal link between molecular gene and phenotype. In at least some cases, different alleles at a single locus can make the difference between an organism having and not having a particular trait. So if a person has a particular allele at such and such a locus, he or she will in the huge majority of circumstances develop Huntington’s disease (Lodish, Berk et al. 2008, p.200). Other monogenic traits in humans — most of which involve serious health consequences — include sickle cell anemia, cystic fibrosis and albinism (Hartwell, Hood et al. 2000, p.26). If we think of the genome as a set of instructions for the building of an organism it is attractive to think of the bases at the relevant locus as somehow representing the monogenic trait in the adult organism.

Of course, it is not the case that all, or even many, traits are caused by variation at a single allele. As Dawkins (1979) notes, in most cases the genotype acts more like a recipe for a cake than a blueprint for a machine. Different parts of a blueprint correspond to different parts of the

¹⁴ It would be a very weak representationalist claim to say that the whole of the genome represents the whole of the organism but that no part of the genome represents any particular part of the organism. It would not be a nonsensical claim. After all, all symbolic representational systems have some atomic symbols that are not composed of other symbols and so have no internal structure. But if this is all we have, we could perhaps say that there is representation by the genome but hardly that there is representation in the genome.

machine, but different ingredients or procedures rarely correspond to different parts of the cake. Still, in some cases, changing one ingredient or one procedure *can* reliably make a particular difference to a particular part of the cake — the crust, the base — and so we might nonetheless be tempted to see that ingredient or procedure as representing the relevant characteristic of the final cake.

Similarly, we might naturally ask whether in at least some cases, particular molecular genes represent particular phenotypic traits. How does this work with a teleosemantic account of representation?

4.2.1 Genes for traits

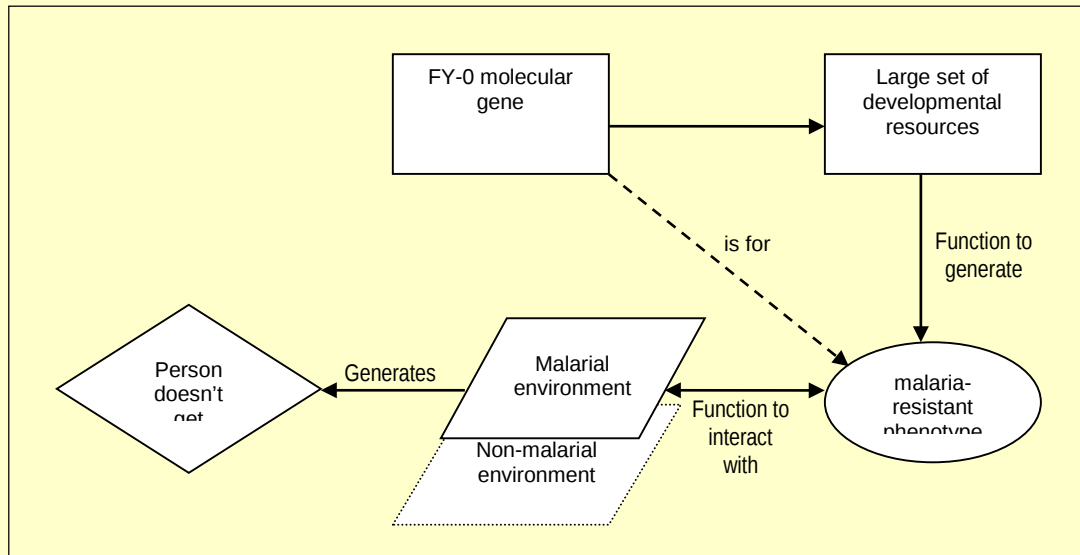
Before we look for representation itself, it may be useful to consider the weaker notion of a gene ‘for’ a trait.

There are some molecular genes that are very closely associated with a particular fitness-enhancing trait, and whose distribution in the population of the relevant species makes it seem overwhelmingly likely that the gene has been selected for its causal contribution to the development of that trait.

A well-known example is the *FY-0* gene in humans, which prevents the synthesis of the FY protein. The absence of this protein confers a degree of protection against the malaria parasite *Plasmodium vivax*. The *FY-0* gene is extremely rare in populations where malaria has not historically been a problem but, for example, is present in nearly 90 per cent of the population in Sub-Saharan Africa (Kaplan and Pigliucci 2001). There is little doubt that, in that region at least, it is the function of this gene to confer protection against malaria. Kaplan and Pigliucci use our standard notion of biological function to define a gene ‘for’ a trait: a gene for a trait is a gene whose biological function it is to contribute to the development of that trait.

- o In populations where it occurs frequently, the atypical haemoglobin gene that gives rise to sickle cell anaemia but also confers heightened resistance to malaria conveys (teleosemantic) representational content about malaria resistance. (Griffiths (2001) referring to Maynard Smith’s (2000) ‘concept of information’)

Figure 8: Genes *for* traits



There is no reason why gene complexes marked by complex epistatic interactions could not also have the function of contributing to the development of a particular trait. We do not know enough now to identify the functions of many such complexes but one likely example is the gene complex that regulates flowering in *Arabidopsis thaliana*. Some of the genes inhibit the actions of others. If we assume that such genes have been selected for this inhibitory effect, we would probably have to say that they are ‘for’ inhibiting other genes involved in flowering in particular circumstances (usually, but not necessarily, conditions in the external environment like day length or temperature).

This is a quite demanding characterisation of a gene being for a particular trait, rather than merely associated with it.

- o The molecular gene must have the right selective history. It must have been selected for its role as a difference maker in relation to the trait in question. So it must participate in causally potent biochemical and developmental pathways leading from the gene to the trait.
- o It also needs to have been the subject of natural selection in the species’ recent evolutionary history. Function can fade over evolutionary time (see section 3.1 above) so a temporally distant episode of selection will not be sufficient to underpin the relevant function today, unless the trait has been maintained by ‘purifying’ selection in the period since.

- o The sort of deleterious monogenic examples we looked at earlier — Huntington’s disease and so on — might feed intuitions that some nucleic acid structures represent particular traits, but they clearly fail to meet the functional test we are considering here: ‘whatever functions a gene may have acquired through selective regimes, causing [Huntington’s] is surely not among them’ (Kaplan and Pigliucci 2001, p.193).

So far, so good. We now have a robust and pretty demanding definition of ‘gene for trait X’ that uses the same conceptual apparatus that teleosemantics uses to characterise the representation relationship and we have reason to think that in some cases at least particular molecular genes are indeed for particular traits. Can we take the argument one step further and establish that some molecular genes are not just *for* particular traits but actually *represent* those traits?

4.2.2 Homeotic genes and body plans

There are certainly examples where the relationship between physical patterns in the molecular genes and patterns of traits in the adult organism are correlated by a mapping rule that looks very much like the kind of rule Millikan requires to underpin intentional icons. It is not just that the molecular genes make a crucial causal contribution to the appearance of a particular trait; their physical arrangement along the chromosome corresponds spatially with the arrangement of parts of the adult organism. This seems very much like a (partial) map of the organism, but how does it fit with a teleosemantic account of representation?

Perhaps the best way to proceed is to investigate in some detail an example that seems to offer relatively good prospects of instantiating the genetic representation of phenotypic traits.

In the 1980s, researchers identified a coarse-grained ‘map’ in the embryos of all multicellular (metazoan) organisms. The map corresponds to the pattern along the DNA strands of ‘homeotic’ molecular genes, which control segment-specific differences in all metazoa, despite the 650 million odd years since their common ancestor was alive (Lodish, Berk et al. 2008, p.969).

These are genes in which mutations give rise to transformations of complete body regions in the organism. For example, in the *Antennapedia* mutant of *Drosophila*, the antennae on the head of the fly are transformed into an additional pair of second legs (Gehring and Hiromi 1986). In *Drosophila*, mutations in homeotic genes may result in a fly with two pairs of wings rather than a fly with one pair of wings and one pair of small, rounded balancing organs (‘halteres’).

Homeobox genes are a subset of the homeotic genes that act as a template for the synthesis of transcription factors that play a crucial role in development. They are a highly conserved family of DNA sequences that are associated with homeotic and segmentation genes of *Drosophila*.

Homeobox sequences are highly conserved in other animals, including mammals (Garcia-Fernandez 2005). *C. elegans* has about 85 homeobox genes, *Drosophila* has around 120 and humans have around 235 (Holland, Booth et al. 2007).

Among homeobox genes, hox genes are the best studied. They control the patterning and specification of compartments along the anterior-posterior body axis (the 'head to tail' axis) and are generally clustered together on a chromosome (Epstein, Pillemer et al. 1997). The order of the genes in the cluster corresponds with the areas of their function along the animal's anterior-posterior axis: the genes at the 3' end of the hox cluster correspond to the anterior part of the body and the genes at the 5' end, the posterior. This holds in insects as well as vertebrates (Burglin 2006, p.25).

Similar phenomena arise in plants, where a particular type of homeobox genes play a key role in establishing the anterior-posterior (tip-to-root) axis (Flintoft 2008). The axis is set up when the zygote divides asymmetrically into a large basal cell, which gives rise to the root system of the plant, and a small apical cell, which gives rise to its shoot system. Each of these two cells produce different cell lineages.

In general, during the development of a metazoan organism, compartments arise in the embryo but not in the egg, which is anatomically simple. The compartment plan gives each cell its 'address', and location relative to other cells in the body (Kirschner and Gerhart 2005, p.183). Hox genes influence the combination, amount and order of conserved core processes at specific regions in the organism. The compartment array consists of places where different combinations of processes occur in parallel. For example, *Drosophila* is divided into at least eight large compartments.

If you get rid of the Hox genes, the animal still develops the same number of segments but they are not normally differentiated. For example, if the Hox genes are removed from the flour beetle, it develops 14 segments, the usual number, but each looks like a head with an antenna attached (Stuart, Brown et al. 1991).

One thing that makes it plausible that some hox gene represents the seventh body segment in an insect is that we have something that looks like a map. The arrangement of the genes along the chromosome mirrors, in a geometrical way, the arrangement of the body segments, that is, we can find a simple geometrical transformation that will get us from one to the other. The analogy with, say, a street map is close in many ways.

So it is tempting to think that a configuration of homeobox genes, together with the associated regulatory regions, does constitute an instruction to ‘grow an arm here’. But how does this idea fit in with our teleosemantic account of representation?

4.2.3 Millikan

Can we discern teleosemantic content in the hox genes? It seems reasonably straight forward to find teleosemantic content in the street map:

- o the map maker is the producer device;
- o the map is the icon;
- o the person who follows the map is the consumer device;
- o the mapping rule (in Millikan’s terms) is the geometrical transformation that takes the complex three dimensional terrain of the city and transforms it into the much simpler two dimensional map.

But it is a good deal harder to fit the hox genes into a teleosemantic model of representational content. Let us try to apply Millikan’s account of an intentional icon, taking the hox genes as the putative icon. *Mutatis mutandis*, the hox genes in a particular organism will be an intentional icon iff:

- (1) The hox genes are a member of a reproductively established family with direct proper functions.
- (2) Normally, the hox genes in a particular organism mediate between a producer device and a consumer device, the presence and proper functioning of each being a Normal condition for the proper functioning of the other.
- (3) Normally the hox genes adapt the consumer device to conditions in such a way that the consumer device can perform its functions.
- (4) If we take the hox genes to be an imperative intentional icon, it must be the proper function of the consumer device to respond to the hox genes by producing a state of affairs — in this case, a body plan — onto which the hox genes will map.

- (5) If we take the hox genes to be an indicative intentional icon, the Normal explanation of how the hox genes adapt the consumer device such that it can perform its proper functions makes reference to the fact that the hox genes map onto something else'. In other words, it is the function of the consumer to respond to the hox genes in some particular way and it cannot do this, at least not Normally, unless the icon maps onto something else.

Paragraph (1) seems to be satisfied. As usual, we do not know all about the evolutionary history of hox genes but it seems hard to imagine that they do not have the function of ordering the segments of the adult organism. For the sake of argument, at least, let us assume that they do have that function.

Paragraph (2) is more problematic because it is difficult to find plausible candidates for the roles of producer and consumer device. What produces the hox genes? Assuming we are talking about a sexually reproducing organism, we might consider:

- o the entire genomes of the pair of parental gametes;
- o the pair of parental organisms *tout court*; or
- o the pair of sets of hox genes in the parental gametes ('the parental hox genes'), together with the processes of meiosis and gamete fusion that together generate the hox genes in the zygote of the offspring.

The first option seems questionable. If we think that it is a function of the entire genomes of the parent organisms to produce hox genes in their offspring, it must also be the function of the parental genomes to produce each of the twenty odd thousand protein coding genes in the human genome (Pertea and Salzberg 2010) or, indeed, the proteins themselves. That might be right in a weak sense but it makes the parental genomes too much universal producers of representations.

Perhaps more obviously, it is implausible to regard the pair of parental genomes as just one producer device. They are physically separate and are subject to different fates in relation to survival and reproduction. Moreover, on a teleosemantic view, a producer device must have the right function to participate in a representational relationship and it seems hard to find a function for a gerrymandered device like the pair of parental genomes. It is (just) possible that each parental genome has aetiological functions but the pair of genomes surely does not.

The same difficulties attend the second option.

The third option gives us a producer device with a more specific function and so avoids the ‘universal producer’ objection. We might also consider that the pair of parental hox genes is a single device, albeit a short-lived one, with the function of producing hox genes in the offspring.

Even if we think we can live with option (3) for the producer device, we are still left with the question of what the consumer could be. This is harder.

Remember that our original intuition was that genes or sets of molecular genes might represent traits that they are for — in our example, that hox genes might represent the organismal body plans with which they are associated. So we need to find a consumer device that the hox genes somehow adapts so that it can perform its functions.

One option would be to say that the consumer device is the full set of resources that go into the development of the organism but this includes extra-organismal environmental resources — food, shelter, sunlight, oxygen etc. But this collection of items hardly constitutes a single device and it clearly has no biological function — it is not part of a reproductively established family. *A fortiori* it does not have the function of producing a particular type of organism in response to the expression of the hox genes.

Another option would be to say that the consumer device is the genome of the organism, together with other inherited developmental resources, like the maternal cytoplasm, but no extra-organismal developmental resources. Then we need to ask:

- o whether the hox genes in the organism mediate between (a) the parental hox genes, together with the meiotic machinery and (b) the rest of the genome of the organism together with other inherited developmental resources;¹⁵ and
- o whether the presence and proper functioning of the parental hox genes etc. is a Normal condition for the proper functioning of the genome of the organism etc., and vice versa.

I think it is fair to say that the first dot above is satisfied. The parental hox genes, together with the meiotic machinery, produce the organism’s hox genes and these interact with the rest of the organism’s genome and other inherited developmental resources to generate an organism with a

¹⁵ Of course the organism’s hox genes are part of its genome, so in order to keep the representational token and the consumer device distinct, we must take the consumer device to be the rest of the genome of the organism and other inherited developmental resources.

body plan that maps onto the layout of the hox genes. It also seems reasonable to say that the presence and proper functioning of each of the parental hox genes is a Normal condition for the proper functioning of the organism's genome.

But the vice versa part does not seem right. The presence and proper functioning of the organism's hox genes is *not* a Normal condition for the proper functioning of the parental hox genes. Their function is to sort out the body plan of the parents, not to be passed down to the organism. Their function is part of a Normal explanation of their being passed down to the organism but the passing down is not part of their function itself.

To recap, if we take the hox genes of a particular organism as a putative representational token, it does not seem possible to identify producer and consumer devices that are capable of fulfilling the functional roles that, under Millikan's account, they must fulfill if the token is to succeed in representing the body plan with which the hox genes is associated.

4.2.4 Shea

Shea (2007, p.325) argues more broadly that under his account of genetic representation, DNA functions as a token that represents traits according to his teleosemantic model with the following assignment of functional roles:

- o the producer device is the mother and father gametes;
- o the intermediate token is the DNA in the zygote; and
- o the consumer device is 'cellular machinery and environmental factors'.

I think there are also problems here, cognate with the difficulties set out in the previous section.

First, Shea is taking the parents' gametes together as a producer device, but it is hard to see how a particular set of parental gametes could have a single direct proper function.

- o Each of the two molecular genes — one on the mother's gamete and one on the father's — could have a function, if it has been selected for in the recent evolutionary past. In that case, it may be part of a reproductively established family that is there because it has been selected for its contribution to some fitness-enhancing phenotypic trait.
- o The process of meiosis itself could have a biological function. There are a lot of theories about how meiosis arose and what advantages it conferred on the first meiotically

reproducing organisms (eukaryotes) struggling for existence in prokaryotic world (Ridley 2000, p.178). Nevertheless, it seems reasonable to suppose that at some point in the distant past, meiotically reproducing organisms won out over mitotically reproducing rivals, and did so because of some advantage in reproduction that meiosis conferred.

- o But the pair of molecular genes in the zygote — one from the mother of the organism under consideration and one from the father — is not a member of a reproductively established family and so it cannot have a direct proper function.

Second, I cannot see a plausible way to defend Shea's claim that the consumer device is 'cellular machinery and environmental factors'.

An initial difficulty is that the consumer mechanism is hugely variable from instance to instance (Griffiths and Stotz 2013, p.168). How could it be the function of the organism's DNA to interact with any particular combination of the millions of possible combinations of environments and developmental factors?

It could be the function of the organism's DNA to interact with those combinations of the environments and developmental factors that have mostly obtained in evolutionary history. So we could say that it is the function of some insect's DNA to interact with leaf litter and hot, humid conditions — which is the way it has been most of the time throughout the insect lineage's recent evolutionary history — but not with leaf litter and freezing cold conditions — which is the way it has occasionally been in evolutionary history, as a result, say, of volcanic eruptions.

Even if we accept this kind of function for the consumer device, however, we have to face a further difficulty. Under a teleosemantic account, if the zygotic DNA is to represent the phenotype to which it usually gives rise, it must be the function of the consumer device — 'the environment plus developmental factors' — to generate some response to the representational token, the zygotic DNA, that interacts with whatever it is that the representational token represents. It seems to me there are two fatal problems here.

What could this response be? The obvious candidate is a developmental process that starts with the zygotic DNA in the maternal cytoplasm and ends up with the adult phenotype.¹⁶ This seems sort of reasonable. Meiosis happens, the zygotic DNA is generated and enters into immediate

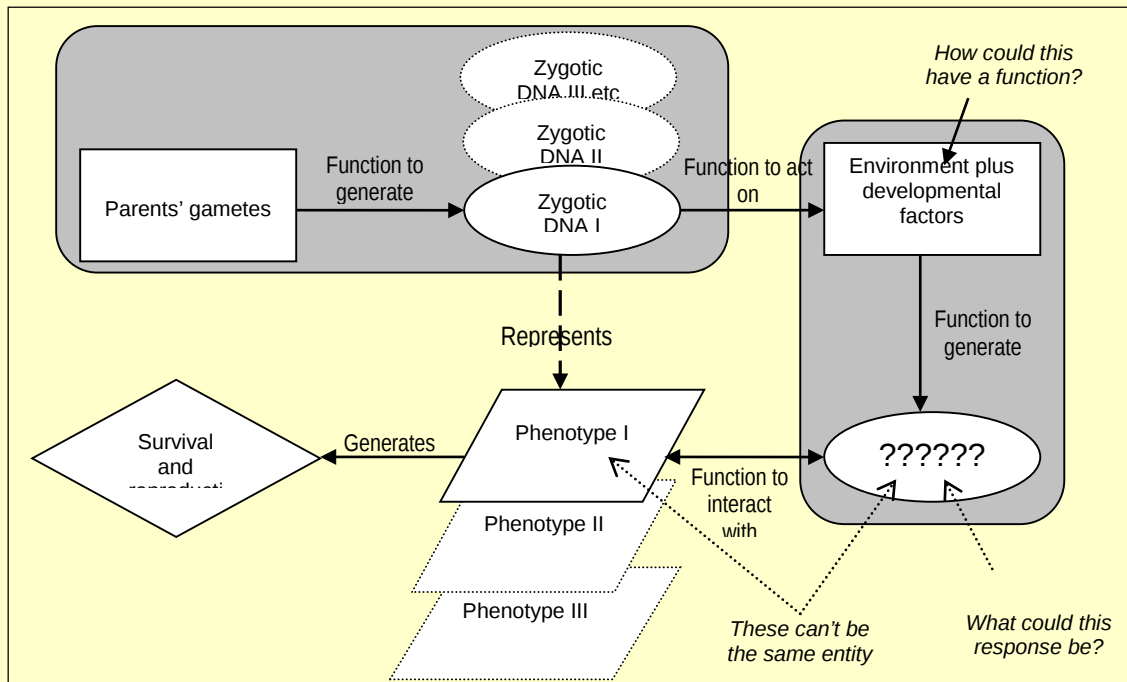
¹⁶ Why the adult phenotype? The organism has to survive throughout its life, at least till the point where it reproduces. So delimiting the response might be a bit tricky.

causal interaction with the environment and other developmental resources, like the maternal cytoplasm, nutrients, other cells (at least in the case of metazoans once cell division has begun), parental care (if any), constructed environmental niches and so forth.

But according to Shea's model the response generated by the consumer device is meant to interact with the represented state of affairs to promote the survival and reproduction of the consumer device (or sometimes both the producer and consumer devices). Clearly the developmental process that culminates in the adult organism does not interact with the phenotype to which the genotype Normally gives rise. It produces that phenotype. Or the phenotype is the final temporal stage of the developmental process. But either way the response is not distinct from the state of affairs that the zygotic DNA is meant to represent.

Perhaps more fundamentally, it is hard to see how the putative consumer device can have any biological function at all. Under the aetiological concept of function with which we are working, the function of *Z* is (roughly speaking) what *Z*'s ancestors have done in the past that accounts for *Z*'s being here now. But here the consumer device is meant to be something like the combination of the environment and other developmental resources that contribute to the organism's development. Some of those developmental resources may be part of reproductively established families but there is no way the extra-organismal environment can be. The developmental resources needed to support the development of a viable organism include food, shelter and a range of affordances within specific ranges — i.e. not too hot, cold, windy, radioactive etc. As we noted above, environmental factors such as these do not have functions. They have not been selected for their capacity to contribute to the development of any organism. The problems are set out diagrammatically in Figure 9.

Figure 9: Can DNA represent phenotypes under Shea's model?



For the reasons given above, I do not think that this putative consumer device can have a biological function in the same way as teleosemantic consumer devices must have.

4.2.5 The 'transmission' sense of information

A twist on the 'genes carry semantic information about phenotypes' story is to say that genes convey information from generation to generation (Bergstrom and Rosvall 2009). This is undoubtedly right if we take information to be natural information.

- o Genes carry natural information about past environments. If we find a long coat gene in a tiger, we reduce our uncertainty about the conditions in which the tiger's ancestors lived. We are more certain than we were that conditions were chilly.
- o Genes also carry natural information about future generations. If we find a long coat gene in a tiger, we reduce our uncertainty about the phenotype of the animal's offspring. We are more certain than we were that they will have long coats.

Moreover, as Bergstrom and Rosvall note (2009, p.167) the hypothesis that it is the biological function of genes to be transmitted across generation seems overwhelmingly likely.

Genes are made out of DNA, a molecule that is exquisitely fashioned so as to (1) encode lots of sequence information in a small space, (2) be incredibly easy to replicate, (3) be arbitrarily and infinitely extensible in what it can say, and (4) be structurally very stable and inert ...

We will see in section 6.3, that the early evolution of nucleic acid structures is far from well understood. Nevertheless, it is hard to resist the idea that at least one biological function of DNA and other nucleic acids is to be passed down from generation to generation (Shea 2011).

If, however, we want to strengthen the claim and say that genes transmit representational content from generation to generation, we strike the same problem we met above when we considered the proposition that genes, or larger units within the genome, represent phenotypes with which they are associated. How could intergenerational representation work in a teleosemantic framework of the kind we have been working with? To bridge the gap between generations, we must take the token that conveys semantic information from producer to consumer to be one of the offspring's genes (or possibly its entire genome). The producer device must then be the parental genes (or the parental genomes).

Now, again, we need to find a consumer device whose function it is to respond to the offspring's genes (or genome) in a way that enables them (or it) to survive and reproduce. And again, there seems to be no device with such a function. The variable complex of developmental resources that, in evolutionary history, has 'consumed' the genes of successive generations of organisms includes an array of environmental as well as inherited resources: air, sunlight, food, shelter, symbionts, membranes etc. This developmental complex has not been selected for — though parts of it may have been — and so has no biological function. Another possibility might be that the consumer device is all of the offspring other than its genome, excluding other developmental resources necessary to the offspring's survival and reproduction (Shea 2011, p.187). Shea argues plausibly enough that identifying the consumer in this way allows us to distinguish between the token (the offspring's DNA) and consumer (the rest of the offspring). But on the other end of our teleosemantic story, difficulties arise.

First, under a teleosemantic account, whether Millikan's or Shea's, we need to find some response that it is consumer's function to generate in response to the token. That is not so easy here. If the consumer is all the rest of the offspring other than its genome, what response does the rest of the offspring generate that allows it to deal with the world it finds itself in? It seems artificial to say it is the offspring's behaviour, which (in most species at any rate) is just as much conditioned by the offspring's genome as is its anatomical phenotype.

Second, we must try to identify the content conveyed by the token. Maybe this is not so much of a problem for Millikan. She can say that it is the proper function of the rest of the offspring to respond to the offspring's genome by producing an offspring onto which the genome will map. Admittedly, she has to sacrifice any distinction between the consumer device and the represented state of affairs: they are the same thing, but perhaps that is tenable. Things are worse for Shea,

who sees the content borne by a representational token as the evolutionary success condition, specific to that kind of token, of the behaviour of the consumer that such tokens prompt. Not only must he abandon the distinction between the consumer device and the behaviour of the consumer device that the token prompts, as we saw in the previous paragraph, but what could possibly be the evolutionary success condition, specific to genomes of the relevant lineage, of the of the organisms in that lineage. There is no such specific success condition.

Shea himself (2013) mounts a slightly different argument that genetic representations are passed down from generation to generation and read in development, based on a version of his infotel semantics. He takes:

- o the producer to be the evolutionary history of the lineage in which a particular gene has been selected;
- o the token to be, in sexually reproducing organisms at least, a particular gene in a particular organism;
- o the consumer to be the process of development of the organism;
- o the consumer's response to be the phenotype that the gene is for; and
- o the content to be the environmental conditions with which the phenotype helps the organism deal.

This is a somewhat different account of representation than in his (2007), which we considered in section 3.2. There, he stipulated:

A representation of type R has content C if:

- (a) Rs are intermediate in a system consisting of a producer and a consumer cooperating by means of a range of mediating representations (all specified non-intentionally), in which every representation in the range also satisfies (a) to (d); ...

Here, there is no requirement that producer and consumer cooperate. At (2013, p.6) he notes that 'unintuitively, the producer is not a single organism, but a whole, temporally-extended episode of natural selection'. A temporally-extended episode of natural selection is not the kind of thing that can itself be selected for, therefore, not the kind of thing that can have a biological function and therefore, not a producer device that can cooperate with a consumer device, given the producer-token-consumer account of representation that we have been working with.

The sense of genetic representation that Shea adopts here is an interesting one, but I am not sure that it can be seen as an instance of a satisfactory account of representation in general (which we would clearly want it to do). If we allow the producer device to be anything at all, we strike the difficulties faced by Jablonka's consumer-centric view of representation (section 3.2.6): too many things end up bearing representational content. If we insist that the producer device has the biological function of producing tokens that elicit a successful response from the consumer, episodes of natural selection will not qualify as producers. There may be a workable middle way of constraining the range of things that can play the role of producer: wide enough to include episodes of natural selection but not so wide as to admit clearly non-representational cases. It is not obvious that no middle way could be found, but the fact that it would have to admit producers like an episode of natural selection — a huge, complex inter-temporal set of events and counterfactuals — without admitting too many producers, certainly suggests that it will not be easy to find.

4.2.6 Conclusions

Under a teleosemantic approach to representational content it is very hard to see how nucleic acid structures can represent phenotypic traits either within one generation or across generations.

Under Millikan's approach, it is hard to see what could play the role of consumer and producer devices in such a way that the content of the representational token can be a phenotypic trait.

Under Shea's approach to the question, which takes the consumer device to be the environment in which the organism develops plus a range of factors needed for that development, it is even harder. First, it is surely impossible for such a portmanteau consumer device to possess a biological function. Second, it is hard to see what the response of the consumer device, which is meant to help the consumer deal with its environment, could be.

If we try to find teleosemantic content in messages passed in the genome from generation to generation, as Bergstrom and Rosvall (and Shea) suggest, we encounter cognate difficulties.

So, as we found with the putative representation of proteins by nucleic acid structures, a teleosemantic approach to representation does not always yield the positive answer we might expect. And again, as I argued in that case, I do not see an unexpected negative as a particularly good argument against teleosemantic theories of representation. Whether we accept a teleosemantic account should depend on how well they deal with core representational systems like natural languages, beliefs, formal languages, maps, blueprints, photographs and so forth. Judgements on cases like molecular genes should be spoils to the victor in the main contest.

4.3 Representing the environment

So far we have considered the relatively modest proposal that some nucleic acid structures represent the proteins for whose synthesis they act as a template and the much less modest proposal that some nucleic acid structures represent the phenotypic traits in whose development they are implicated. But of course many tokens in other representational systems — natural languages, computer models, animal signaling systems etc — represent past, present or future conditions in the environment.

There are many animal signaling cases in which it is the function of the producer to generate an intermediate token in response to some contemporaneous feature of the environment and it is the function of the consumer to respond to the token immediately in one particular way. This is a rudimentary form of representation and many systems much simpler than the human language-making system are capable of performing this kind of representation.

Consider, for example, our friend the vervet monkey:

- o a producer vervet monkey generates three different calls, A, B and C;
- o A usually induces a consumer vervet to look into the air, B usually induces it to climb a tree and C usually induces it to look at the ground;
- o over the evolutionary history of vervets, looking into the air has contributed to the survival and reproduction of vervets when an eagle has been present, climbing a tree when a leopard has been present and looking at the ground when a python has been present; and
- o the generation of an A call covaries with the presence of an eagle, of a B call with the presence of a leopard, and of a C call with the presence of a snake.

The covariation between the response and its associated success conditions need not be perfect, just good enough to ensure that the pattern of responses to the intermediates has been selected for during the consuming system's evolutionary history. Similarly, the covariation referred to in the last dot point need not be, and in fact is not, perfect: vervets, especially young vervets, quite often make mistakes (McCarthy 2004, p.116). It has, however, been strong enough to have contributed, over generations, to the survival and reproduction of the consuming system's ancestors.

There are many examples of such responses to environmental conditions.

- o A rattlesnake has certain cells that engage its hunting routines (Rowlands 1997, p.290). The cells only fire if the snake's infrared detectors, located in its nose, are stimulated and its visual system receives positive input. The first condition is satisfied when there is a source of warmth nearby, the second when something is moving nearby. In the snake's Normal environment the two conditions are satisfied only when there is a field mouse nearby.
- o The female fruit fly mates only once in her lifetime. If a male attempts to court a female fly after mating she will display her ovipositor — a specialised organ for depositing eggs — to the male, at which point he immediately ceases courtship behaviour.
- o 'I see you' signals sometimes co-evolve between predator and prey because, when a prey animal sends the signal to a predator, the prey benefits because it is less likely to be attacked, and the predator benefits because it can avoid wasting time and effort on an attack that is unlikely to succeed. For example, an 'I see you' signal has coevolved between the Asian hive bee, *Apis cerana*, and its hornet predator, *Vespa velutina*: when a hornet approaches a bee colony, guards perform a shaking movement that repels the hornet (Tan, Wang et al. 2012).

Clearly these systems are much simpler than human thought or natural language. The token is produced as soon as the environmental conditions are registered by the producer device and the consumer reacts immediately. The hornet does not register the bee's shaking movement, modify its beliefs about the world and apply them later on to guide its behaviour. If the bee signal is not acted on at that time, it has no effect and makes no contribution to the survival and reproduction of either bee or hornet. In these simpler systems, evolution has not yet decoupled representation from action.

So, these animal signaling cases certainly look like cases where relatively simple systems in non-human organisms succeed in generating pushmi-pullyu representations of the environment. How about molecular genes?

There are two ways that molecular genes respond to environmental conditions. Most fundamentally, some genes are expressed only in particular conditions within or outside the cell: the expression of a gene creates a particular protein that helps the cell deal with the prevailing conditions. I give examples below. In more sophisticated cases, genes responsible for adaptive

phenotypic plasticity can give rise to different morphologies in different environmental circumstances (Via, Gomulkiewicz et al. 1995).

In either of these cases, are molecular genes (or their expression) representing the environment?

The literature reveals differing views. Some advocates of teleosemantics have not been prepared to grant that nucleic acid structures genuinely represent environmental circumstances. For example, Papineau (2003, p.121) says:

Genes, conceived of as sections of DNA, cause the machinery of gene expression to make proteins. If things go well ... these proteins will then give rise to various phenotypic features. So the genes indeed prompt ... causal sequences — which are directed towards biological ends. However, there is nothing in this akin to the gearing of these causal sequences to variable environmental circumstances. Normal genes do not indicate that, since circumstances are such-and-such, the way to achieve some result is to do X rather than Y. They simply dictate the construction of some given protein. Given this, it seems to me that genes can at best be regarded as brutally imperative representations ... However, such brute imperatives, unaccompanied by any states designed to gear instructions to circumstances, do not seem to me to qualify as serious representations. Any state with a function, any state designed to produce some effect, could be viewed as such an imperative.

Papineau contrasts molecular genes — where he claims that the causal sequences to which they contribute are not geared to variable environmental circumstances — with a human desire like the desire to drink. In the drinking case, the concentration of salt in my body exceeds some threshold beyond which damage to my tissues is likely to ensue, this activates osmoreceptors in my subfornical organ, which excite higher integrative centres in my brain where my conscious experience of thirst probably arises (McKinley and Johnson 2004). My desire to drink is geared to environmental conditions — specifically, salty conditions — inside my body.

The contrast is misconceived. On the one hand, Papineau is advancing an implausibly complex and demanding characterisation of representation. It is surely too much to require any representation to indicate that ‘since circumstances are A, the way to achieve result B is to do C rather than D’. A Millikanish or Sheaish communication-based model of representation is demanding enough.

On the other hand, I think he is exaggerating the consequences of attributing representational content to simple pushmi-pullyu representations. Admitting pushmi-pullyu representations as genuine representations — albeit ‘brute imperatives’ — does not entail that *any* state with a function can be viewed as a brute imperative (see section 3.2.3 above). On the theories of

representation that we are considering, the attribution of representational content relies on a producer-token-consumer functional structure that does not arise whenever a state has a function. It is the liver's function to clean the blood but in doing so it does not generate tokens whose function it is to affect the activity of any consumer device: it is not possible to view the liver, or its behaviour, as an imperative representation, no matter how 'brute'.

I shall show below that the causal sequences involved in protein synthesis are very often triggered by environmental circumstances. Molecular genes for the production of hundreds of enzymes and gene regulation proteins are expressed in response to changing conditions in the cellular environment and in the environment external to the organism.

Let us consider how protein synthesis in response to environmental conditions within the cell — if such synthesis exists — could fit Shea's teleosemantic account of representation. In general terms, if mRNAs are to represent particular conditions within the cell, Shea's account of representation requires that:

- (1) It is the function of a producer device — here, DNA, RNA polymerase and the spliceosome, which is an assembly of small nuclear RNAs (snRNAs) and around 50 proteins — to generate intermediate items — mRNAs (Hartwell, Hood et al. 2000, p.238).
- (2) The mRNAs impact causally on a consumer device — the ribosome and tRNAs — which responds systematically to each mRNA by linking together amino acids attached to tRNAs to form a particular protein determined by the sequence of codons in the mRNA.
- (3) The consumer device has an evolutionary history that associates with each protein particular 'evolutionary success conditions' — here, the cellular conditions that trigger transcription — in which, over the device's evolutionary history, the protein has contributed to the survival and reproduction of the device's ancestors.
- (4) The generation of an mRNA covaries with the cellular conditions that trigger transcription.

A concrete example is the expression of the *lac* genes — *lacZ*, *lacY* and *lacA* — which metabolise lactose in prokaryotic cells.

- (1) It is the function of relevant regions of DNA, RNA polymerase and the spliceosome to generate a polycistronic mRNA corresponding to the three *lac* genes (Hartwell, Hood et al. 2000, p.538).¹⁷
- (2) The mRNA impacts causally on the consumer device, which consists of the ribosome and tRNAs. The consumer device responds systematically (and performs its adapted function) by linking together amino acids attached to tRNAs to form three enzymes — β -galactosidase, permease and transacetylase — each of which is determined by the sequence of codons in the polycistronic mRNA.
- (3) The consumer device has an evolutionary history that associates with the production of the enzymes particular ‘evolutionary success conditions’ — in this case, the presence of lactose in the cellular environment — in which, over the system’s evolutionary history, the enzymes have contributed to the survival and reproduction of the system’s ancestors (by metabolising the lactose and thus generating energy to maintain the cell’s processes).
- (4) The generation of the particular mRNA covaries with the presence of lactose in the cellular environment (through the effect of allolactose on the nuclear DNA).

With this assignment of roles in the Shea model, the sequence of bases along the mRNA does not represent the protein for whose synthesis it characteristically acts as a template, or any trait in whose development the protein is implicated, but specifically some particular condition in the cellular environment.¹⁸ This clearly fits the model of a coordination problem where the consumer’s uncertainty about what to do, given its uncertainty about the state of the world is resolved (or at least diminished) by a representational token sent by the producer.

¹⁷ A cistron is a sequence in an mRNA molecule (a ‘coding region’) that acts as a template for the synthesis of a single protein. Many bacterial mRNAs include the coding regions for several proteins (enzymes in this case) that function together in the one biological process. Most eukaryotic mRNAs are monocistronic (Lodish et al 2008, 217).

¹⁸ Note that RNA polymerase and the snRNAs and proteins that constitute the spliceosome are themselves synthesised on a pattern supplied by a DNA template, so both the producer and consumer devices are DNA driven, but this does not mean that it is the DNA itself that bears representational content. Indeed, in this case it is the mRNA that bears representational content rather than the DNA that acts as the template for its production.

The relationship between the coding regions on the DNA and the mRNA is like the relationship between occurrent and non-occurrent beliefs. Both the DNA and the underlying mental states that allow the generation of occurrent beliefs have the potential to generate tokens that represent states of affairs — particular cellular conditions in the DNA case or particular states of affairs in the world in the case of the mental states — but they do not actually do so until triggered, either directly by the environment or some more indirect way.

For example, although at all times I would, if asked, assent to the proposition that a normal adult aardvark is bigger than a normal adult vole, I have not represented the aardvark as bigger than the vole until I have tokened the thought. Similarly, while it is at all times the function of the DNA *lac* genes to act as the template for the synthesis of β -galactosidase, permease and transacetylase when lactose is present in the cellular environment, it is only when they are expressed and a polycistronic mRNA tokened that the presence of lactose is represented.

Note that this case, where the expression of a molecular gene or genes represents some feature of the cellular or broader organismal environment, differs from the earlier case where we considered whether mRNAs might represent the proteins for whose synthesis they act as a template. In that case, our functional view did not extend past the synthesis of the protein at the ribosome. Consequently, Millikan's account did attribute simple pushmi-pullyu representation to the mRNAs, while Shea's account, which emphasises the evolutionary success conditions of the consumer's response, did not. In this case, the functional structure within which gene expression takes place includes the broader environment of the cell, and the organism.

Note too that in cases of gene expression in response to conditions in the cellular environment, as in the animal signaling cases, the kind of signaling we find is neither imperative nor indicative but both at the same time. It makes no contribution to our understanding of these processes to attribute to the mRNA transcribed from the *lac* genes the indicative content 'lactose is present in the cellular environment' without also attributing to it the imperative content 'synthesise β -galactosidase, permease and transacetylase'. In both cases we have what Millikan calls 'pushmi-pullyu' representations (section 3.2.6).

4.3.1 Misrepresentation

A crucial characteristic for any system that generates representational content is that a representational token generated by the system may be false, if indicative, or may not be complied with, if imperative (Dretske 1995).¹⁹

For Millikan, an imperative intentional icon is not complied with if the consumer device does not respond to the icon by producing a state of affairs onto which the icon maps. An indicative intentional icon misrepresents when the icon does not map onto the state of affairs that it needs to map onto in order for the consumer device to perform its function. In the case of a cell producing a particular gene product in response to a change in the cellular environment, which is a pushmi-pullyu case, misrepresentation on both fronts arises when nothing is produced, or when the wrong product is produced.

This could happen for any one of a number of reasons. Something could be wrong with the promoter region that is meant to initiate transcription. Errors in transcription, in processing of the primary transcript or in translation at the ribosome could mean that the wrong product is synthesised. But even if one of these things happens and the consumer fails to benefit from the generation of the token, the token will still possess the functions that characterise a pushmi-pullyu representation.

Shea's characterisation also allows misrepresentation to arise. This happens when:

- o the token carries natural information that a particular state of affairs obtains;

¹⁹ We have discussed misrepresentation as a desideratum for a general theory of representation, in section 3. The issue did not arise in the consideration of Shea's model in section 4, which dealt with the possibility that nucleic acid structures could represent proteins, nor in section 5, which dealt with the possibility that they could represent phenotypic traits, because the problem in those cases was that there was no plausible way of identifying a consumer device in a suitable functional structure. In the case of the representation of proteins under Millikan's model, it could be that transcription errors, or faulty processing of the primary transcript or mistranslation at the ribosome means that the protein we end up with does not correspond to the relevant stretches of DNA. In such a case, the mature mRNA will not adapt the activity of the ribosome and associated machinery so that they can perform their proper functions, and misrepresentation will have occurred.

- o an evolutionary explanation of the current existence of the representational system adverts to tokens of the relevant type having carried natural information about that state of affairs; and
- o the state of affairs is the evolutionary success condition for the behaviour that it is the consumer's function to generate in response to the token; but
- o the state of affairs does not obtain.

Even with the addition of the condition that the token carry natural information that a particular state of affairs obtain, it is clearly possible for the first three conditions to hold without the relevant state of affairs obtaining:

- o natural information is not infallible;
- o an evolutionary explanation of the current existence of the representational system can advert to tokens of the relevant type carrying natural information about the relevant state of affairs without that state of affairs obtaining now; and
- o an evolutionary success condition is a state of affairs that has prevailed often enough (but not necessary always) in the evolutionary past to underpin the selective function of the consumer device — but it does not have to obtain now.

Both Millikan's and Shea's teleosemantic models allow for misrepresentation when the expression of a molecular gene is representing particular cellular conditions.

4.3.2 Conditions outside the cell

So far, in exploring how nucleic acid structures might represent conditions in their environment, we have concentrated mainly on conditions in the immediate environment: the presence of lactose, concentrations of invasins etc. For Millikan, these are the conditions that it is the function of the consumer device to bring about (in the imperative case) or the conditions onto which the state of affairs generated by the consumer device is supposed to map (in the indicative case). For Shea, these are the evolutionary success conditions, the conditions with which the consumer's response is supposed to deal.

A natural question to ask, and one which has received plenty of attention in the teleosemantic literature, is at what level we should locate the content of a representation. In some sense it seems sensible to stick to the immediate chemical conditions within the cell: they are the conditions with the most direct causal connection with the consumer's response. But if the immediate

chemical conditions within the cell are usually caused by particular conditions in the broader extra-cellular environment, it also seems natural to say that the consumer's response represents those broader conditions.

For example, in plants, osmotic stress arises when there is a sudden change in the concentration of solutes, especially salt, around a cell, causing a rapid change in the movement of water across the cell membrane. When there is a high concentration of salt in the surrounding solution, water is drawn out of the cell through osmosis, thus 'shocking' the cell. When there is a low concentration of salt, water enters the cell in large amounts, causing it to swell and burst (Kultz 2007).

Osmotic stress, particularly due to drought, is one of the most serious problems that limits growth and crop productivity. Under osmotic stress, many plants accumulate 'osmolytes' in their cells, small molecules dissolved in the cytoplasm that maintain cell volume (Yancey 2001). These include proline, glycine, betaine and sugar alcohols (Yoshida, Kiyosue et al. 1997). Proline is probably the most widely distributed osmolyte: its accumulation has also been observed in bacteria, invertebrates, protists and algae.²⁰

So when proline is synthesised and levels of proline increase in the cell, our standard story may be taken to suggest that the synthesis represents the dry conditions prevailing in the organism's current environment.

This potential extension, though, does raise a question about whether we can ascribe determinate content to particular mRNA tokens. To take a familiar, non-genomic example, consider a frog whose visual system produces a particular kind of signal when a fly (or any other small, dark object) passes in front of its eyes. Does the signal represent a fly or a small dark object more generally? More appositely in this case, does the signal represent the fly or the properties of the light that reaches the frog's eyes (Price 2001, p.106)? Similarly, we might ask what the expression of genes that act as a template for the synthesis of proline represents. Is it dry conditions in the external environment or osmotic stress in the cellular environment?

I think that the expression of the relevant genes represents osmotic stress in the immediate environment, rather than drought conditions in the external environment, because it is the

²⁰ Archaea — evolutionarily ancient prokaryotic microorganisms that often live in extreme environments like brine ponds, thermal vents and the digestive tracts of cows — rely on inorganic osmolytes like potassium.

function of the gene expression to deal with osmotic stress, not drought conditions, even if, in the evolutionary history of the relevant lineage, osmotic stress has arisen mostly as a result of drought conditions in the external environment.

In the history of the lineage, we may suppose for the sake of argument, there has very often arisen a causal chain of this kind: drought conditions in the external environment → osmotic stress → expressing the relevant molecular gene → synthesis of proline → osmotic rebalancing → cell survival → organismal survival and reproduction. The items in the second half of this chain, from ‘expressing the relevant molecular gene’ onward, constitute an analysis of the consumer’s response. As Neander (1995) notes, the items are linked by a ‘by’ relation. The response promotes the survival and reproduction of the organism *by* ensuring cell survival *by* osmotic rebalancing *by* synthesising proline *by* expressing the relevant molecular gene.

We can accept that all of these items are functions of the gene expression, but when it comes to determining the content of a representational token, that is not specific enough. We need to find a way to determine where in the causal chain the function of the gene expression resides.

We can eliminate the last two element of the chains, cell survival and organismal survival and reproduction, on the grounds that on an aetiological characterisation of function everything with a function must in the end contribute to reproductive success. Representational content would be indeterminate with a vengeance if we accepted either of these. This, however, still leaves us with an embarrassment of riches.

This is a complex issue, and to explore all the options fully would go beyond the scope of this essay, so I confine myself to saying that I think Neander is on the right track in preferring the lowest level of functional analysis at which the consumer’s response as a whole is an unanalyzed component (1995, p.130). It makes more sense to see the content as the presence of osmotic stress than as drought conditions. Drought may have been the main cause of osmotic stress in evolutionary history, but the expression of genes for the synthesis of proline would have (and probably has at one time or another), assisted the organism to survive and reproduce just so long as osmotic stress were present, no matter what the cause of the stress. If the organism ingests a lot of salt, the cellular conditions will be similar to those typically arising from drought, yet the chemical pathway that leads to the synthesis of proline will still help the organism deal with those conditions.

A parallel with the frog case might arise if there were two types of flies, species A and B, in the frog’s evolutionary history, and species A were much commoner than species B. In this case, it is better to see the function of the frog’s tongue snap as capturing flies rather than just species A:

the capturing of both species has contributed to the survival and reproduction of members of the frog's lineage.

On this basis, I think we should see the function of the expression of the proline genes as dealing with osmotic stress in the cellular environment rather than the more remote drought conditions in the external environment. And therefore we should see the content of the expression as osmotic stress rather than drought conditions.

4.3.3 Recapitulation

Under teleosemantic view of representation, whether Millikan's or Shea's, we find that features of the environment, especially the immediate environment within the cell, are represented by genomic processes and in particular, by the expression of molecular genes that give rise to gene products that allow the cell and the organism to deal with the conditions they confront.

The most obvious possibility is that genomic processes could represent conditions in the cellular environment. This fits a teleosemantic account well. It is not hard to find examples where a nucleic acid structure in an organism's DNA responds, often through complex regulatory pathways, to particular conditions by generating an mRNA token that triggers the synthesis of a protein that helps the cell (and the organism of which it is a part) deal successfully with those conditions. In such cases we can identify producer and consumer devices which, it is very likely, have been selected for their capacity to participate in the appropriate producer-token-consumer interactions. So when such a system tokens an mRNA that acts as a template for the synthesis of an appropriate protein, the mRNA fulfils the role of a token that represents the relevant cellular conditions.

There is a strong case that gene expression is representing immediate conditions in the cellular environment, but we should also consider the possibility that it is also representing conditions in the distal environment. This is certainly not out of the question *prima facie* but, as Neander argues, it seems more attractive to restrict the contents of environment representations to the lowest level of functional analysis — i.e. the most biologically specific level — at which the consumer response as a whole is an unanalyzed component. In the case of osmotic stress, this is the production of osmolytes by the cell, which may be in response to a range of environmental conditions, of which drought is only one.

5 More sophisticated representational capacities

So far I have been claiming only base-grade pushmi-pullyu representational status for gene expression. The function of the expression of a particular molecular gene is both:

- o to map onto the cellular conditions to which it is a response; and
- o to adapt the activities of the cell to those conditions.

In other words, it both says ‘chemical compound *X* is present’ and gives the instruction ‘synthesise enzyme *Y*’.

Still I think that on either Millikan’s or Shea’s account of representation, it is reasonable to conclude that some genetic processes go beyond the synchronous, cooperative communication between producer and consumer mechanisms that characterises most pushmi-pullyu representation. In particular, I think that:

- o some genomic processes — particularly patterns of gene expression in circadian and other biological clocks — can represent future events; and
- o some genomic producer devices practice deception by inducing a response in consumer devices in circumstances where it is not the function of the consumer to produce that response.

These are, so far as I know, new claims about the representational capabilities of genomic processes, and I will therefore devote a fair amount of space to setting out and defending them.

5.1 Future representations

A core characteristic of any sophisticated representational system is that particular representational tokens can refer to events in the future and the past as well as the present. Such a capacity is not necessary for representation to arise at all but a system that represents only contemporaneous states of affairs is clearly quite inflexible. As a matter of fact, I believe that some genomic processes do represent future events.

In a teleosemantic model of representation, the temporality of a representation may be cashed out in terms of the temporal relations between token production, token consumption, response and success condition. In the systems we have looked at so far, it has been the function of the producer device to generate a token that causes the consumer device to generate an immediate

response and it is the function of that response to interact immediately with the token's evolutionary success condition.

So, in the case of the vervets, under Normal conditions, the production of a token (e.g. an eagle cry) is contemporaneous with its success condition (the presence of an eagle). The production of the token is followed immediately by the consumer's response. So, under normal circumstances an eagle is in the vicinity when the first vervet produces its cry. It might take a few milliseconds for the sound waves to make their way to the consumer's ear, a few more to get to the cerebellum, the reticular formation and the thalamus and a few more to get from these areas to the cortex. From there, via primary, secondary and motor areas, the consumer's response, looking into the air, again follows swiftly.

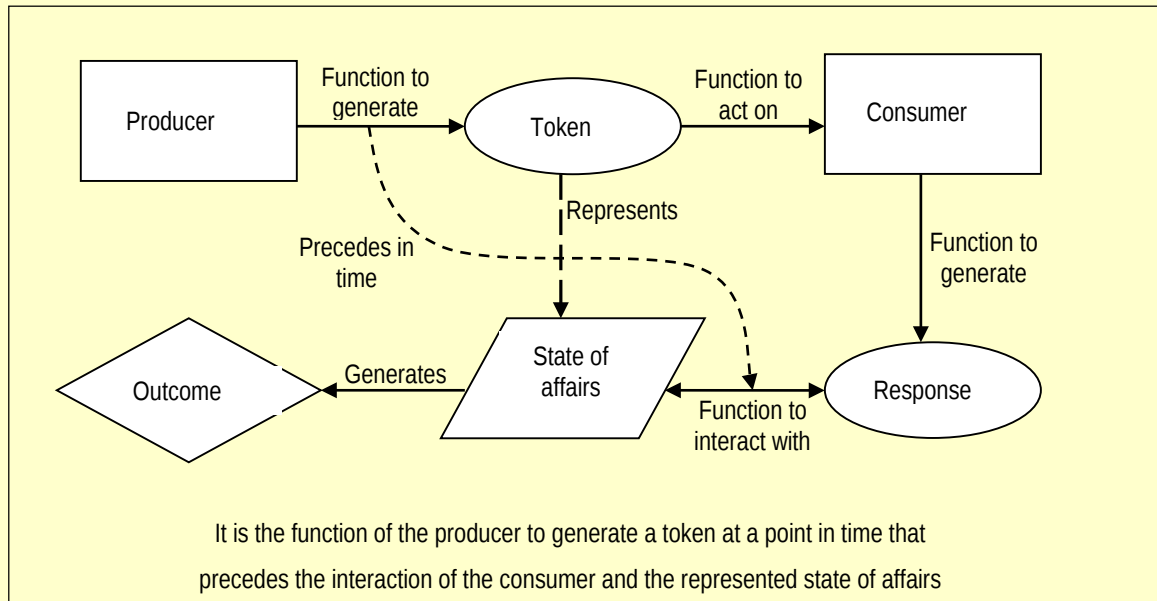
Tokens of this kind may be thought of as being in the present tense because in evolutionary history, the presence of the success condition has been contemporaneous with the generation of the token. Similarly, the polycistronic mRNA produced in response to the presence of lactose in the cellular environment has helped the consumer device (the ribosome) when lactose is present at the time the mRNA is produced.

In the case of a future tense token, it is the biological function of the consumer to produce some response to the token, not at the time the token reaches it, but at some later time. So Alcibiades might say to Bias, 'when the sun sets, say a prayer to Hecate.' The function of this statement is to induce Bias to say a prayer to Hecate, not when he hears Alcibiades but when the sun sets.

Figure 10 sets out a teleosemantic structure for a future representation.²¹

²¹ The diagram is based on Shea's model, but I think that under Millikan's model we also find future imperative content in the functioning of the genetic clock. The phosphorylated proteins mediate between the producer device (the genetic clock) and the consumer device (the system that generates mating routines or heightened metabolism or whatever) and it is the function of the consumer device to respond to the tokens by producing a state of affairs that maps onto the tokens temporally, i.e. at a particular time in the future. So I think that we have future imperative representation here, by Millikan's lights.

Figure 10: Representing a future state of affairs



5.1.1 Genetic clocks

Phenomena with the functional structure illustrated in Figure 10 appear at the genomic level, where a genetic clock, dependent on the regular expression and inhibition of particular molecular genes, controls a number of crucial processes.

The suprachiasmatic nucleus is a part of the hypothalamus (a portion of all vertebrate brains located just above the brain stem). The central genetic clock is located in the suprachiasmatic nucleus but clock genes in other tissues are also able to control the timing of biological processes.

These circadian timekeeping mechanisms are clearly of adaptive importance.

- o Experiments with *Arabidopsis* and with the bacterium *Synechococcus elongatus* show a clear selective advantage for organisms whose timekeeping mechanisms are ‘in tune’ with day and night in the environment.
- o Chipmunks with lesions to the suprachiasmatic nucleus are more likely to be active during the hours of darkness and fall prey to weasels during that period (DeCoursey, Walker et al. 2000).
- o Fruit flies with non-functioning *period*, *timeless*, *cycle* or *Clock* genes have low quality sperm. Mating between couples with non-functional clock genes have 40 per cent fewer offspring than wild type flies (Beaver, Gvakharia et al. 2002).

5.1.2 Entrainment

In the examples considered below, a regular process controlled by the clock genes triggers a particular process in the organism at regular intervals. It might be thought that the chemical token that finally triggers the process is simply conveying a present imperative representation at that point in time, so that nothing is representing a future state of affairs. The process of *entrainment*, however, ensures that the time-keeping mechanism can trigger the response of the consumer mechanism at a variety of times after the point of entrainment. Entrainment is the setting of the genetic oscillator to match environmental cycles, of light and dark, or of temperature (Barak, Tobin et al. 2000).

The biological function of the entrainment mechanism in the organism's clock genes is to register changes in environmental cycles by altering the periodicity of the genetic clock so that the consumer's response is triggered at a time that corresponds with a particular *future* state of affairs in the environment. It is this plasticity in the timing of the consumer's response that creates the distinction between present and future genetic representation. If we take the entrainment mechanism as the producer device, the instruction conveyed by the producer changes from 'you, leaf, unfold in 12 hours' time' to 'you, leaf, unfold in 13 hours' time'.

In both cases, the function of the tokens is to ensure that the leaf unfolds when daylight comes but the entrainment mechanism changes the timing of the consumer's response in the future.

We will consider three examples.

5.1.3 Breeding cycles in mammals

In mammals, a timing system based on clock genes monitors day length and causes the animal to mate at a time of the year that ensures that birth occurs during mild weather and that the offspring's key growing period coincides with ready availability of food (Boden and Kennaway 2006, p.379). Generally, this means that the animal gives birth in early spring. When mating characteristically occurs, then, depends on the gestation period of the particular species. The mammalian timing system has three main elements:

- o the retina, which registers light, and at least three associated neural pathways that connect to the suprachiasmatic nucleus;
- o a self-sustaining molecular clock; and
- o an output pathway that connects with peripheral organs.

The mammalian clock components are not directly photoreceptive: light signals from the retina are transmitted through neurons to a number of transcription factors that regulate gene expression (Wijnen and Young 2006).

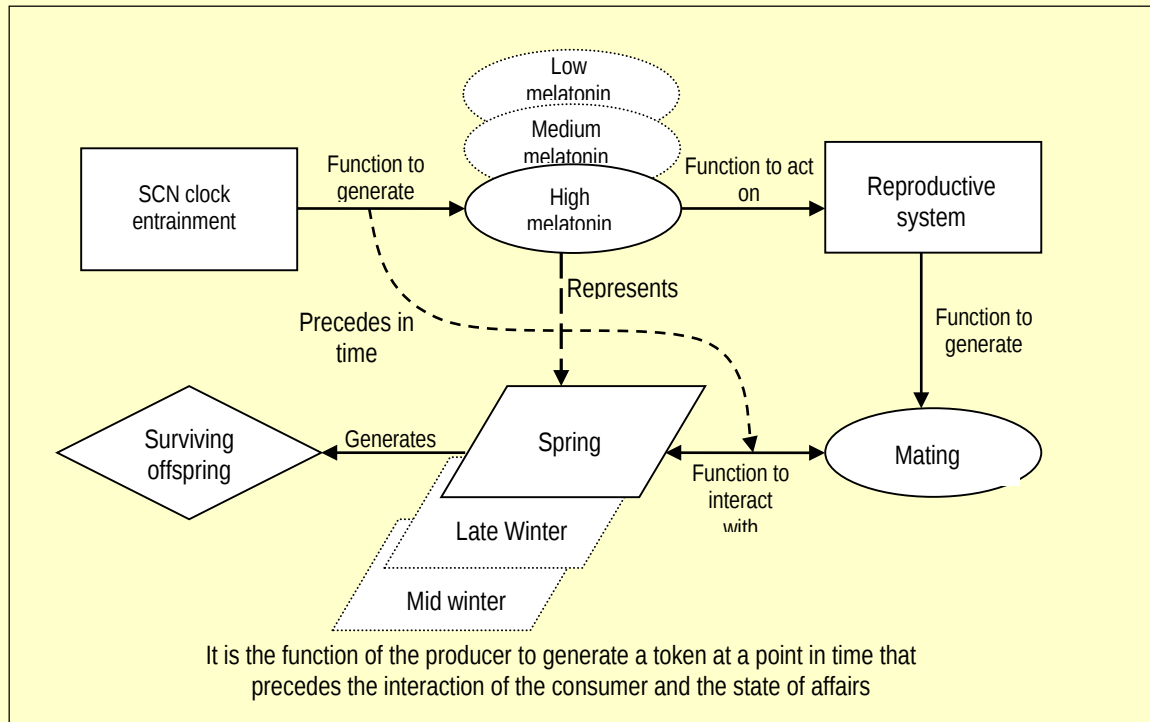
The core of the clock is a negative feedback loop where a pair of clock genes act as a template for the synthesis of proteins that bind to and block the operation of proteins that activate the transcription of the clock genes. In other words, the clock genes produce proteins that dampen their own activity. When the level of clock gene products falls sufficiently the transcriptional activators increase the rate at which they initiate transcription of the clock genes and the level of clock gene products increases again.

The output mechanism is the daily secretion of melatonin by the pineal gland. Once melatonin levels reach a certain level, the reproductive system is triggered and breeding behaviour ensues. Provided the systems involved are properly performing their functions, high melatonin levels coincide with long days and the approach of warmer weather. Of course the system does not always work. Human researchers can trick hamsters into mating at the wrong time and longer days are not always accompanied by the ready availability of food. The teleosemantic account, however, finds representation in the biological functions of the relevant systems, and these depend on evolutionary history, not current performance.

The crucial point is that this clock system is entrained by the light-dark cycle, through activation of the *Per1* and *Per2* genes in the suprachiasmatic nucleus. This means that the signals passed from the clock to the consumer mechanism — in this case the reproductive system — are not running according to an invariable timetable. The timing varies with the environment so that the producer device is effectively predicting when the consumer device should produce its response.

If particular environmental cues change, the clock is entrained to the new conditions and the message it sends to consumer device changes in its timing, as it might be from ‘mate when the days are 13 hours long’ to ‘mate when the days are 14 hours long’. If it were not for this capacity for variable entrainment, it would be possible to argue that the clock mechanism is not sending messages about what should happen in the future but that it is merely running through a predetermined cycle which has the function of coinciding with particular conditions in the environment. In other words, without entrainment the producer device would not have a range of different signals that it can send to represent particular states of affairs. The result would be that animals could not adjust to different seasonal cycles — e.g. an 11 hour night at one latitude is not at the same time of year as an 11 hour night further north. As it is, though, it is the function of the consumer device to generate a response after the entrainment process, that allows the organism to deal with a future state of affairs.

Figure 11: Variable timing of mating behaviour in hamsters



5.1.4 Circadian rhythms in plants

The clock in *Arabidopsis thaliana* controls a large number of biological processes: gene expression, calcium levels in the cytosol, chloroplast movement, the opening and closing of the stomata and the petals, the movement of cotyledons and hypocotyl length.²²

It consists of a set of transcriptional feedback loops that include a number of DNA-binding proteins as well as a number of additional regulator proteins (Yanovsky and Kay 2002). Light affects red light receptors and blue light receptors that in turn affect (a) the expression of molecular genes that act as templates for two of the DNA-binding proteins and (b) the

²² A chloroplast is a 'green organelle found in the cytoplasm of the photosynthetic cells of plants and algae, and in which the reactions of photosynthesis take place' (Lawrence 2005, p.115). Stomata are 'minute openings in epidermis of aerial parts of plants, esp. on undersides of leaves, through which air and water vapour enters the intercellular spaces, and through which carbon dioxide and water vapour from respiration is released' (Lawrence 2005, p.630). Cotyledon(s) are the first leaf or leaves of the embryo in seed plants. The hypocotyl is the part of the stem below the cotyledons in a plant embryo (Lawrence 2005, p.311).

degradation of regulator proteins through a cycle of phosphorylation and dephosphorylation.²³ Proteins encoded by clock genes repress their own expression by blocking transcriptional activators that act as positive elements in the feedback loop. A weaker concentration of clock proteins alleviates inhibition of the transcriptional activators and restarts the oscillator cycle (Barak, Tobin et al. 2000).

The leaves of many types of plants, including *Arabidopsis*, have an open configuration during the day, allowing them to catch as much light as possible, and a closed configuration at night. If the plants are transferred to an environment with constant light, the regular leaf movements continue. However, the circadian cycle can become entrained by environmental cues. So, for example, if the length of the dark-light cycle changes, the circadian clock will become synchronised with the new day length.

Suppose that:

- o a plant is running on a 24 hour circadian cycle with 12 hours of light and 12 hours of darkness;
- o the light-dark cycle changes to 13 hours of light and 11 hours of darkness;
- o the plant's circadian cycle is entrained to the new light-dark cycle;
- o if the plant were transferred into a constant light environment, it would continue to run on the new cycle.

The cycle is responsive to the environment. The function of the entrainment mechanism is to ensure that the leaves uncurl at a time in the future when light is available for photosynthesis.

So during the entrainment process, when the light receptors register the onset of darkness, the producer mechanism is effectively telling the leaves, 'this time, uncurl in 12 hours and 10 minutes time', 'this time, uncurl in 12 hours and 20 minutes time' etc.

5.1.5 Restricted feeding entrains clock genes in mice

If a mouse is kept in constant darkness and fed only once a day, it soon 'learns' when its next meal is going to be (Hara, Wan et al. 2001). Several hours before the meal, it begins to run

²³ Phosphorylation is the covalent addition of a phosphate group to a molecule, in this context, to a protein.

around more, its body temperature goes up and its levels of corticosterone increase.²⁴ Since the mouse is kept in darkness, it is clearly not getting cues from the light-dark cycle. It can only be the change in feeding regime that recalibrates the metabolic rhythms, with entrainment taking around six days to take hold.

Genetic and molecular studies have established that gene expression feedback circuits are crucial to the generation of circadian rhythms. From the work of Hara et al, it is clear that there are at least two types of genetic clock oscillator, the light-entrainable oscillator found in the suprachiasmatic nucleus and the feeding-entrainable oscillator for which at least some genes are expressed in the liver and other organs apart from the suprachiasmatic nucleus.

The expression of circadian clock genes in the liver does not rely on the suprachiasmatic nucleus. Mice with lesions of the suprachiasmatic nucleus evinced the same entrainment as intact mice in response to restricted feeding. In both sets of mice, the clock genes in the suprachiasmatic nucleus were unaffected.

The content of the instruction here is something like ‘get ready to eat in 24 hours time’. (Of course, as with the hamsters or the flax, the mouse may not be fed in 24 hours time: the food may come before or after or not at all.)

The selective story behind food entrainment is less well understood than the story behind the light entrainment that underpins the first two examples. However, it appears that synchronizing biological processes with the likely availability of food is important for the maintenance and replacement of the protective epithelial barrier in the gut, gut immunology and the production of digestive enzymes (Bron and Furness 2009).

5.1.6 Conclusions

We do not know much about the selective processes that have given rise to the clock genes and the associated molecular machinery so we cannot say for certain that it is the function of the clock genes to adjust the systems with which they interact with environmental cycles. However, given the fitness gains that accrue from synchronisation between the genetic clock and the environment it seems very likely that the genetic clock and its capacity for environmental recalibration are evolved traits with that function. At the least it seems almost certain that the

²⁴ Corticosterone is a steroid hormone produced by the adrenal glands which gears up lipid, carbohydrate and protein metabolism.

clock has been stabilized for this function, in that mutations that degrade the working of the clock are weeded out by selection; and this is enough to underpin the necessary biological function.

On this reasonable assumption, it is the function of the various organismal responses to correspond temporally with events — especially the rising and setting of the sun or particular times of the year — in the extra-organismal environment. Moreover, in the cases considered here, it is the function of most of the tokens — the phosphorylated and dephosphorylated proteins — to induce a response, not at the time the token is produced but at some time in the future. In this, the tokens produced by the clock genes perform the same kind of future imperative function as a utterance of ‘when the sun comes up, feed the cow’. Its function is to induce a response from the hearer, not at the time the token is generated but at some specific future time.

The repeated phosphorylation and desphosphorylation that constitute the process at the heart of the genetic clock correspond to the ticks of the second hand on the clock face of a time bomb. The function of the ticks — with the exception of the tick that takes us from 11.59.59 to 12.00.00 — is not to detonate the bomb but to mark off a period of time so that the bomb will be detonated at some future time.

So I think that on a teleosemantic view, the signals controlled by the genetic clock genuinely refer to future times, just as some linguistic tokens do in natural languages.²⁵

²⁵ The tokens generated by the genetic clock bear representational content on both Millikan’s and Shea’s accounts. The main difference between the two is that Shea’s account is more demanding, and limits the content of representational tokens to the evolutionary success conditions associated with the consumer device’s response. But that doesn’t mean that the tokens bear content under one account but not the other, although we might think that the tokens have somewhat different content under the two approaches. Let’s take the mammalian mating example. For Shea, the tokens issued by the clock genes represent the warm weather that, all going well, will attend the birth of the lambs and the first months of their lives. For Millikan, the content could be richer: if (as seems reasonable) we take the clock tokens as imperative representations, then the Millikan content could be the broader state of affairs that includes the thriving lambs (who do not appear in Shea’s picture). But in either case, the clock tokens bear future representational content.

5.2 Deception

Not only can genomic phenomena misrepresent the state of the environment, they can ‘deliberately’ mislead other genes.

This should not come as a surprise. Animals deceive one another all the time. There are several groups of birds which trick other birds into raising their young for them. Cuckoos are the most famous. Crows sometimes mimic humans in order to attract chicks, which they eat (McCarthy 2004, p.110). Chimps, gorillas and baboons use a variety of techniques to mislead conspecifics (Byrne and Whiten 1992, p.614). Even tiny crustaceans in the Caribbean employ bluff to hold onto their holes in the rocks (Steger and Caldwell 1983, p.558). It seems very likely the behavioural mechanisms that generate these deceptive performances are evolved mechanisms and that generating such deceptive performances is one of their biological functions.

So if we think that there is semantic communication that benefits the consumer going on at both the organismal and genetic levels, and that there is semantic deception that benefits the producer but not the consumer going on at the organismal level, we should perhaps look to see whether we find deception at the genetic level as well.

To start with, it is important to appreciate that deception is more than just misrepresentation, which can arise where any causal factor intervenes to prevent the producer or the consumer from performing their functions in the right circumstances. For instance, the consumer might be injured, or some external event might occur that prevents the token from reaching the consumer (a sudden gust of wind blowing away the monkey’s cry, a heat shock destroying the relevant cell), or the token may be damaged in transmission so as to be ‘unreadable’ by the consumer. Any number of events may intervene to prevent the producer and consumer from performing their mutually adapted functions.

To distinguish deception from misrepresentation, we need some extra ingredient. This may be supplied by the function of the producer device. In the Millikan model, deceptiveness of an intentional icon is largely a matter of abnormality. That is, we have a situation where Normally:

- o intentional icons (call them *Gs*) mediate between producers (call them *Fs*) and consumers;
- o the proper functioning of each is a Normal condition for the proper functioning of the other;
- o the intentional icon adapts the consumer so that it can perform its functions; and

- o (for an imperative icon) it is the function of the consumer to respond to the icon by producing a state of affairs onto which the icon maps;

but, in the case of deception:

- o deceptive producers (call them *Hs*) produce *Gs* — and it is their proper function to do so;
- o consumers respond to the *Gs* as they Normally would if the *Gs* had been produced by *Fs*, that is, by creating a state of affairs onto which the *Gs* map; and
- o the state of affairs that the consumers create benefit the *Hs* (and not necessarily, though possibly, the consumers).

Similarly, Shea's model of representation can be adapted to accommodate deception. Remember that in Shea's version of teleosemantics, accurate representation arises when:

- o a producer device performs its biological function (or one of its functions) by generating different kinds of intermediate tokens that impact causally on a consumer device;
- o the consumer device performs its function (or one of its functions) by responding systematically to each kind of token;
- o the consumer device has an evolutionary history that associates with each response, evolutionary success conditions in which the response has contributed to the survival and reproduction of the system's ancestors;
- o the production of a token covaries with the success condition associated with the response that is characteristically provoked by the token.

Starting from this point, I suggest that a Shea-style account would see deceptive representation as arising when:

- (1) there are some producer devices — call them *Fs* — whose function it is to generate tokens of various types — call them *G₁s*, *G₂s* etc — that impact on a consumer device;
- (2) the consumer device performs its function (or one of its functions) by responding systematically to each *G* token;

- (3) the consumer's evolutionary history associates with each response success conditions in which the response has contributed to the survival and reproduction of the consumer's ancestors;
- (4) it is the function of a family of deceptive producer devices — not *F*s, but *H*s — to produce a G_i token that elicits from the consumer the response it is its function to display in response to a G_i that is produced by an *F*; but
- (5) instead of the consumer benefiting from this behaviour (as has often enough been the case when *G*s have been produced by *F*s), the producer benefits and the consumer does not.

It is not essential that:

- o in any particular case — the consumer is harmed by consumption of the token; or
- o it is the function of the producer device to harm the consumer;

just that it is the function of the producer to generate a token in circumstances where the evolutionary success conditions associated with the consumer's past responses do not obtain.

Let's consider three examples.

5.2.1 *Agrobacterium tumefaciens*

Agrobacterium tumefaciens is a pathogenic bacterium that causes tumours in most species of dicotyledonous plants — flowering plants, in which the embryo has two seed leaves — and in some monocots, causing 'crown-gall disease'. The tumour produces opines — smallish organic molecules formed by condensation of an amino acid and a keto acid or a sugar — which the bacterium uses as a source of energy and carbon.

A. tumefaciens can live in the soil independently of hosts but its genome includes a 200 kilobase plasmid, a portion of which — called 'transferred DNA' or 'T-DNA' — can be transferred into the cells of a host plant.²⁶ So effective is the mechanism that geneticists use *A. tumefaciens* as a

²⁶ A plasmid is a small DNA sequence replicating independently of the chromosome within a cell. They are most commonly found as small circular, double-stranded DNA molecules in bacteria, but are sometimes found in archaea and eukaryotes.

‘gene vector’, since pretty much any DNA cloned into the T-DNA can be transferred into host plant cells.

We have a reasonably good understanding of the biological mechanisms behind the production of the T-DNA, its transportation into the host cell and its importation into the host cell nucleus, but the way in which the T-DNA is integrated into the host genome is less clear (Tzfira, Li et al. 2004). Nevertheless, recent work has suggests the importance of host proteins involved in DNA repair and maintenance. In particular, it appears likely — though not certain at this point — that the VirD2 protein synthesised by *A. tumefaciens* functions as:

- o a component of a site-specific endonuclease in the bacterial cell — that is, an enzyme that cleaves the bacterial DNA at specific sites; and
- o a DNA ligase in the host cell — i.e. an enzyme that catalyses the joining together of two DNA strands. In this case VirD2 mimics the function of the host cell’s indigenous DNA ligase (Ulker, Li et al. 2008).

The second of these functions effectively co-opts the DNA repair enzymes of the host cell into incorporating the bacterial T-DNA into the host genome, so that:

- o the host cell’s transcriptional and translational machinery is used to synthesise opines, which feed the bacterium; and
- o the host’s processes of cell replication also replicate the T-DNA that has been incorporated into the host genome.

In the first case, the bacterial DNA engages the host’s machinery of gene expression even though it is clearly the function of that machinery to express host molecular genes, not the DNA of another species (in another kingdom, no less). In the second, the bacterial DNA induces the nucleic acid structures that participate in meiosis to interact with it so that it is replicated along with the host’s own DNA.

It seems clear that this case constitutes deception in teleosemantic terms, but it may be worthwhile working through the details of both the Millikan-style and Shea-style accounts of deceptive representation.

First, let us consider the Millikan-style analysis, under which *A. tumefaciens* is deceiving the protein synthesis machinery of the host cell because, Normally:

- o host mRNAs mediate between DNA coding regions and the ribosome;

- o the proper functioning of each is a Normal condition for the proper functioning of the other;
- o the mRNA adapts the ribosome so that it can perform its functions; and
- o for an imperative icon — it is the function of the ribosome to respond to the mRNA by building a protein onto which the mRNA maps; while
- o for an indicative icon — the Normal explanation of how the mRNA adapts the ribosome so that it can perform its proper functions makes reference to the fact that the mRNA maps onto host DNA.

In the case of deception, however:

- o bacterial DNA (together with host RNA polymerase and the spliceosome) produce mRNAs;
- o the ribosome responds to the mRNAs as it would if the mRNAs had been produced by the host cell's own transcriptional machinery, i.e. by building proteins (in this case, opines) onto which the mRNA maps; and
- o the opines benefit the bacteria, not the host cell.

So deception prizes apart the imperative and indicative aspects of the pushmi-pullyu representation. The ribosome responds Normally to the mRNA with which it is presented, so it complies with the imperative content of the message it receives. On the indicative side, however, the Normal explanation of how the mRNA adapts the behaviour of the ribosome so that the ribosome can perform its proper functions makes reference to the fact that the mRNA maps onto host DNA. By contrast, in the deceptive case, the mRNA is mapping onto bacterial DNA, not host DNA as it Normally does. The mRNA is, one might say, lying to the ribosome (though, of course, the mRNA does not know that it is doing that).

The Shea-style analysis is a little different, because Shea restricts content to environmental conditions. We can nonetheless discern deception perpetrated by the bacterium on the host cell:

- (1) we have producer devices, DNA coding regions, whose function it is to generate mRNAs of various types that affect a consumer device (the ribosome and associated translational machinery);

- (2) the ribosome performs its function by responding systematically to each mRNA that reaches it (i.e. by building a protein that corresponds to the base triplets on the mRNA);
- (3) the ribosome's evolutionary history associates with each protein synthesised success conditions in which the protein has contributed to the survival and reproduction of the ribosome's ancestors;
- (4) it is the function of a family of deceptive producer devices — bacterial DNA (together with host RNA polymerase and the spliceosome) — to produce mRNAs that induce the consumer to perform its function by building a protein that matches the mRNA (in this case an opine); but
- (5) instead of the consumer benefiting from this behaviour (as has often enough been the case in evolutionary history, when opines have been synthesised to assist in the metabolism of lysine), the bacteria benefit and the host cell does not.

While both the Millikan-style account and the Shea-style accounts of deception find deception arising in this kind of case, they will arrive at different conclusions about what the deceptive content might be. In the Millikan case, the producer device is most naturally seen as sending an imperative token, compliance with which does not benefit the consumer, as it Normally would. In the Shea case, the deception indicative content is something like 'there's lysine around that needs metabolising (so make me an opine)'.

5.2.2 Type III secretion systems

The means by which the T-DNA of *A. tumefaciens* is introduced into the host cell is known as the Type IV secretion system but other bacteria use other systems to breach host cell defences and these depend on deceiving host cell systems.

Type III secretion systems are deployed by bacteria like *Shigella* (responsible for bacterial dysentery in humans), *Salmonella* (enterocolitis), *Bordetella* (whooping cough), *Yersinia* (plague), *Vibrio* (diarrhoea) and *Pseudomonas* (pneumonia). Their function is to deliver virulent bacterial proteins (effectors) into eukaryotic cells. The effectors often display sequence, structural and functional similarities to eukaryotic proteins (Coburn, Sekirov et al. 2007).

The core element of the system is a needle-shaped structure which facilitates the passage of the effectors through the bacterial envelope. It is made up of a multi-ring base, which anchors it to

the envelope, and a needle-like projection that protrudes several nanometres from the bacterial surface.

The mechanics of the delivery of effectors into the host cell are not perfectly understood but we do know that once they are in, they can interfere with a wide range of host cell functions: actin and tubulin dynamics²⁷, gene expression, cell death and cell cycle progression (Galan and Wolf-Watz 2006).

For example, both *Yersinia* and *Salmonella* introduce tyrosine phosphatases into the host cell. These proteins dephosphorylate, and thus put out of commission, two host cell proteins that play a crucial role in getting host cells to stick together ('cell adhesion'). This prevents attacks on the bacterium by host macrophages (large cells that ingest invading microorganisms and scavenge dead cells). The bacterial phosphatases have nucleotide sequences and three dimensional folds that are very similar to those of host phosphatases (Stebbins and Galan 2001, p701). The cell adhesion proteins respond as they would Normally respond to host cell phosphatases — they are deactivated — but in cellular conditions where this response benefits the *Yersinia* or *Salmonella* cells rather than the host cells.

Another example from *Salmonella* involves the delivery into the host cell, via a type III secretion system, of two related bacterial proteins. These proteins activate the synthesis *by the host cell* of proteins that lead to substantial rearrangements of the host cytoskeleton and subsequent internalization of the bacterium into the host cell. Once inside the cell, *Salmonella* actively contributes to the restoration of the normal architecture of the host's cytoskeleton by delivering another effector protein which, in a precise matching of host cell function, shuts down the pathways by which the original pair of bacterial proteins were introduced into the cell.

In these cases, bacterial proteins mimic host cell proteins and evoke from the host cell responses that would Normally accompany circumstances other than those that actually obtain. The indicative half of the pushmi-pullyu representation misrepresents cellular conditions, not because of some random malfunction of the host cell's machinery but as a result of the bacterium's genome performing its proper functions. The indicative content is something like 'cellular conditions obtain that would Normally call for:

²⁷ Tubulins are globular proteins. They are the main constituents of the microtubules which, in eukaryotic cells, form part of the cell scaffolding (the 'cytoskeleton'), which is essential to maintaining cell structure. Actins make up microfilaments, another component of the cytoskeleton.

- o in the first example — the dephosphorylation of the cell adhesion proteins; or
- o in the second example — rearrangement of the cell's cytoskeleton.'

5.2.3 Retroviruses

Retroviruses, like the Rous sarcoma virus (RSV), are composed of RNA and contain a sequence that acts as a template for the synthesis of the reverse transcriptase enzyme. This enzyme, as its name suggests, uses viral RNA as a template for the generation of complementary DNA, reversing the usual process of transcription in which DNA acts as a template for the generation of complementary RNA. This DNA is then integrated into the DNA of a host cell, sometimes causing the formation of a tumour that kills the host organism (Moss 2003, p.136).

This is a case where the producer, the combination of viral RNA and reverse transcriptase, performs its biological function by generating a token, the complementary DNA, which affects the consumer device, the ribosome of the host cell, in a way that is usually harmful to it (when the host organism dies, so does the host cell and its ribosomal machinery). As we noted above, this of itself does not constitute deception: it is the function of the hawk to harm the dove but there is no deception involved.

But in the RSV case, the DNA produced by the viral RNA and its reverse transcriptase is incorporated into the DNA of the host cell. Viral offspring are generated by transcription of this integrated DNA, using the reproductive machinery of the host cell (Vogt 2009). This method of replication defines the family of retroviruses.

So in this case, the DNA produced by the Rous sarcoma virus is usurping the place of the indigenous DNA of the host cell. It is clearly not the function of:

- o the host cell to become cancerous; or
- o the host's RNA polymerase to transcribe the DNA of other organisms; or
- o the host cell's ribosomes to translate into amino acids mRNA transcribed from alien DNA.

These are not things that the ancestors of any of these three systems have done that have helped account for their survival and reproduction. Instead, the viral DNA becomes part of a deceptive producer device that sends mRNA signals — with a content something like 'the host molecular gene that acted as a template for the transcription of this mRNA has been expressed as a Normal

response to prevailing cellular conditions’ — to the host’s translational machinery and perpetuates a cancer cycle that is ultimately fatal to the host.

5.2.4 Conclusions

I do not think there’s much doubt that genomic deception of the kind described in the preceding sections is an important factor in evolutionary history. Organisms like *A. tumefaciens*, bacteria that rely on Type III secretion systems, and RSV, depend entirely on their capacity to send molecular signals to the genomic machinery of their hosts that elicit responses in circumstances where it is not the function of the consumer device to respond.

In some bacterial cases convergent evolution between host and pathogen has seen the pathogen taking genes (and the proteins that they encode) that are already available and then adapting them to a new function. Such a protein typically has a different three dimensional architecture from that of the molecule it mimics, but has evolved to imitate the chemical groups on the surface of its functional homologue in the host.

Bacterial pathogens using these deceptive strategies to batten on host organisms have been hugely successful in evolutionary terms and are clearly capable of wiping out large swathes of host populations when the conditions are ‘right’. It is hard to see how we are to explain the evolution of these biological phenomena if not in terms of selective functions.

A question I will address in section 9 is whether there is additional explanatory force in describing these process in representational terms, such as ‘deception’, rather than contenting ourselves with talk of biological functions. I believe that there is, but I will leave the question for now.

5.3 Recapitulation

It seems clear that most nucleic acid structures that bear representational content are what Millikan calls pushmi-pullyu intentional icons. They are neither indicative nor imperative, but both at once. The response is temporally immediate and the token does not participate in any inferential processes in order to evoke the response. But in some cases, genomic phenomena display more sophisticated representational capacities.

- o First, genetic clocks control biological processes in pretty much all multicellular organisms and can be synchronized to ensure that particular processes coincide with future conditions in the cellular (or broader) environment. Under our teleosemantic

account of representation, these processes represent the future conditions that they are meant to help the organism deal with.

- o Second, a teleosemantic account of deception also seems to fit a number of common biological scenarios. Suppose we have a family of producer devices and a family of consumer devices participating in a producer-token-consumer relationship of the usual teleosemantic kind. Then suppose we have a second family of producers whose function is to produce the same kind of tokens but in circumstances where the responses of the consumer devices benefit the second family of producers rather than the consumers. Then we have an entirely plausible account of deception in a teleosemantic framework. And in practice, there are many examples where one organism deceives another by using the second organism's genetic machinery for the first organism's benefit. Bacteria and viruses both do this.

6 **Compositionality, arbitrariness and the limits of genomic representation**

This essay is largely concerned with the question whether, on a teleosemantic view of representation, particular genomic phenomena bear representational content. But crucial to the representational capacities of genomic phenomena (if they exist) is not just whether they bear content, but the physical structure of the systems that allow them to do so. The physical makeup of these systems determines what kinds of content they are able to bear and the roles that representational content is able to play in the individual organism and other biological systems.

In particular, the physical structures of the genome determine whether representation in the genome is symbolic, compositional and ‘digital’ as against pictorial, non-compositional and ‘analogue’. In this section I will argue for the former view and explore some of its consequences.

At the outset it is important to be clear that DNA and other nucleic acid structures have two related but distinct biological roles.

First, they are a developmental resource. That is, they are one of the resources that usually contribute to the development of a viable organism. Not all developmental resources are necessary to the development of a viable organism: fish to eat are a useful developmental resources for humans but they are not necessary. DNA and other nucleic acid structures, however, are essential developmental resources for all organisms.

Second, they are an inheritance mechanism. That is, they are — at a minimum — a developmental resource that is passed down with variation from generation to generation. All inheritance mechanisms are developmental resources: if something has no impact on the development of an organism, it cannot in any plausible sense be part of an organism’s inheritance from the previous generation. Not all developmental resources, however, are inheritance mechanisms: sunlight is a necessary developmental resource for most plants, but it is not in any sense passed down from generation to generation.

So whether we are considering nucleic acid structures as representing the cellular environment in a developmental context, or the ancestral environment in an evolutionary context, we will find that compositionality and the arbitrariness that underpins it are crucial to the representational power and flexibility of nucleic acid structures.

6.1 Compositionality and unlimited representation

Like paradigmatic representational systems such as natural languages, nucleic acids display compositionality. That is, an effectively infinite number of genomic sequences — in DNA and the various kinds of RNA — can be made up from a small number of basic units.

The enormous number of different sequences made available by this means — and the fact that these differences are ‘read’ and responded to in the developmental process, i.e. the fact that each has the potential to play a different causal role in an organism’s biology — give nucleic acid structures great versatility as a developmental resource, an inheritance system and (so I argue) a representational system. In particular, I will argue that their flexibility underpins greater representational capacities than are underpinned by other systems (see section 7).

Szathmáry and Maynard Smith (1997, p.555) characterise the difference between the compositional nucleic acid mechanism and other, less flexible mechanisms, as a distinction between ‘limited’ and ‘unlimited’. Most inheritance mechanisms and other developmental resources are limited systems because they can only vary over a limited number of states. For example, habitat imprinting can only lead organisms to choose between a limited number of different habitats; DNA methylation can only turn existing DNA sequences on or off. By contrast, the nucleotide bases of the genetic code (like the phonemes of a natural language) can be put together in vastly many different combinations. So the number of possible states is much higher, i.e. genes have the capacity to signal a hugely larger range of phenotypic outcomes (Griffiths 2001, p.404).

While this ‘unlimitedness’ arises by virtue of the compositionality of the genetic code, it is distinct from it. We would still have an unlimited representational system (and inheritance mechanism) if a vast number of representational tokens with different functions in a producer-token-consumer functional structure had arisen in some other, non-compositional manner. For instance, if:

- o eighteenth century preformationists like Everard were right and a tiny pre-existing germ that possesses all the complexity of the adult organism, crystallises in the fertilised egg at a single moment after conception (Bowler 1971, p.224); or
- o representation and inheritance were ‘dose dependent’, so that what was inherited depended (perhaps in part) on the amount of material passed on from parent to offspring;

we could still have an unlimited inheritance mechanism and representational system, so long as the range of tokens available and the functional relationships into which they were able to enter, were sufficiently large.

Natural languages display the same kind of syntactic unlimitedness as nucleic acid structures. Sentences in a natural language are composed of words. In agglutinating languages, at least, words are composed of morphemes (Lyons 1977, p.73), as in *un-by-pass-abil-ity*. There are a very large number of morphemes but each is composed of a much smaller number of phonemes — 40 in English, 11 in Polynesian and 141 in Khoisan, the click languages of southern and eastern Africa (Pinker 1994, p.171). At all levels of the structure, the compositional relation at work is concatenation. Each word is a finite string of morphemes, so that exactly one morpheme (the first) is the successor to no morpheme in the word, exactly one morpheme (the last) has no successor in the word and each morpheme that is not identical with either the first or the last morpheme is the successor to exactly one morpheme in the word and has exactly one morpheme in the word as its successor. Similarly a morpheme is a string of phonemes and a sentence is a string of words. Quine (1946) provides a formal account.

The parallel with the structure of the genetic code is obvious enough. In sequences that are able to function as a template for protein synthesis ('coding regions'), bases are strung together in triplets ('codons') along the DNA molecule. Each triplet, determined just by the bases and their order, corresponds to an amino acid, or to the termination of transcription. Triplets are strung together to form longer sequences that correspond to a protein. The order of the triplets on the DNA strand is the same as the order of the corresponding amino acids in the completed protein.

A number of larger, higher order structures have also been identified.

- o In some cases, especially in bacteria and archaea (but also in nematodes), coding regions are linked together in operons, which are under the control of a single regulatory structure and give rise to polycistronic mRNA that acts as a template for the synthesis of a number of different protein products that act in the same biochemical pathway (Blumenthal and Gleason 2003).
- o In others, a set of very closely linked genes, a 'supergene', contribute to a particular trait. Recombination between the genes is suppressed so that disadvantageous combinations do not arise. The genes responsible for mimicry in some species of butterfly are the best understood example (Charlesworth and Charlesworth 2011).

- o Co-adapted gene complexes can also arise, where selection favours a co-evolved set of alleles that optimises individual survival and reproductive success (Burton, Rawson et al. 1999). The Major Histocompatibility Complex in immune systems is a well-known example.

Coding regions, operons, supergenes and gene complexes — together with regulatory regions and stretches of DNA whose biological function, if any, is unknown — are grouped together in chromosomes. So we can identify at least five cumulative levels of concatenation within the genome of an organism: base, codon, coding region, higher level units and chromosome.

By contrast, a discourse — taken to be a sequence of sentences — has at least six levels — discourse, sentence, phrase, word, morpheme and phoneme — and the genome has five — but this does not vitiate the parallel.²⁸

- o First, where we decide to stop counting levels is, to some degree, arbitrary. We could, for instance, describe a fourth level of the genetic code by joining together the strings corresponding to the proteins that are involved in a particular cellular process (which might include a number of coding regions and operons) into a longer string, a ‘process-string’. Or we could stop our description of natural languages at the sentence level.
- o Second, even if we cannot find a natural stopping place in our description of both structures that gives each the same number of levels, the parallel between them remains. In both cases, we start with a small number of atomic items, string them together into larger units, string those units together into larger units and so on. Whether we stop after three or four or fourteen iterations, the basic structure — an iterated process of concatenation of atomic elements into longer and longer strings — is the same.

Compositionality is a structural property of great importance that is characteristic both of paradigm representational systems like natural language and of the genome. A system that generates difference by varying the linear order in which a small number of simple units are

²⁸ An obvious difference between the two is that there is nothing in the genome that corresponds to a conversation. Crick’s central dogma (see section 4.1.4 above) ensures that the genome does not display that same bi-directionality as natural languages: molecular genes cannot converse with one another. But that’s a different issue from the one I am looking at here.

arranged can take advantage of a combinatorial explosion to create a multitude of different entities in an economical and flexible way.

Compositionality itself relies, of course, on the availability of a structuring relation like concatenation. The other essential ingredient in the compositionality of both molecular genes and natural language sentences is the fact that both:

- o the production, transcription and translation of molecular genes; and
- o the production and reception of sentences in natural languages;

are what Haugeland (1987, p.53) calls 'digital systems'.

Such a system is a set of positive and reliable processes that produce and re-identify tokens from some fixed set of types. The distinction between positivity and reliability is an important one.

Reliability refers to the likelihood of a process succeeding, positivity to the possibility of the process succeeding perfectly. A positive process allows a certain margin of error within which all performances are equivalent and success is total.

- o Compare a poem and a painting. A painting decays over time. Over thousands of years, even with the best care, it changes significantly from the way it was when first painted. A poem on the other hand can be perfectly preserved. It may not be, of course: errors in transcription may creep into successive copies. That is a matter of reliability. But because the poem is the product of a digital system, it is possible for it to be perfectly preserved in a way that the painting cannot be.
- o Compare a bishop move in an over-the-board game of chess and a serve in a game of table tennis. If the bishop settles upright in the corner of a square it has made *exactly* the same move (for chess purposes) as it would have made had it settled in the centre of the square. The table tennis serve is different. If the ball had landed on the table one centimetre to the right or left, it would not have been exactly the same serve for table tennis purposes: it would in all likelihood have been harder or easier for the receiver to return.

Szathmáry and Maynard Smith (1997, p.559) make the same distinction between what they call 'modular' and 'processive' replicators. Clark and Wheeler (1996, p.10) note that compositionality is necessary to underpin 'a full inner code' rather than just 'an isolated inner sign'.

We might ask at this point if there is a limit to compositionality of either nucleic acid structures or of the discourses of natural language, i.e. whether there are the same type of constraints on their length. In theory:

- o you can make a well-formed sentence as long as you like just by conjoining other well formed sentences with ‘and’; and
- o you can generate indefinitely many well formed sentences without ‘and’ in them just by incorporating as large a natural number as you wish (spelled out in words, if necessary).

Of course, there is an upper limit to the length of a sentence that can actually be embodied: after a while the universe runs out of quantum events.

Whether a genome can, in principle, be of indefinite length seems more difficult to say. There do not appear to be many constraints on the structure of a genome. It can have thousands of repeated bases and very long sequences of bases that do not code for any protein or, so far as we know, have any other biological function. For example, the protist *Amoeba dubia* has 200 times as much DNA per cell as *Homo sapiens* and it is clearly not all coding for protein synthesis (Lodish, Berk et al. 2008, p.223). So maybe a genome can, in principle, be of any length. In practice, of course, there is some (unknown) nomological upper limit for the length of a genome, just as there is for the length of a sentence.

In sum, the finite/infinite distinction between sentences (or discourses) and genomes doesn’t seem very important, even if we were to conclude that a sentence can, in principle, be indefinitely long and a genome, in principle, cannot be. In both cases, the limits to the length of representational tokens, if any, are enormously liberal, so that ‘unlimited’ seems a harmless exaggeration if it is an exaggeration at all.

6.1.1 What if proteins were the templates for more proteins?

Godfrey-Smith (2000) sets out a thought experiment in which we discover that instrumental genes are not nucleic acid structures like DNA sequences but the same proteins as participate in metabolic processes in the cell. Elsewhere (2000, p.205), he maintains that in such a scenario there would be no arbitrariness in the functioning of genes. While he does not give a detailed argument for this claim, the analysis of arbitrariness set out below explains why his intuitively attractive conclusion holds. In this system, it would not be nomologically possible for one protein to act as a template for the synthesis of another: the producing mechanism depends on generating a protein from a sample of the same protein. The templates for protein synthesis are iconic, not symbolic. An *A* token is the only possible template for the production of another *A* token.

Godfrey-Smith thinks that ‘Removing genetic coding from the world need not change much else, and this gives support to my claim that we should only think of coding as part of an explanation of how cells achieve the specific task of putting amino acids in the right order.’

I think this is overstating the case. It is true that coding is not the whole of the explanation of how cells put amino acids in the right order. In order for a cell to do that it is necessary for there to be a functioning cell. The rest of the cellular machinery necessary for protein synthesis — RNA polymerase, spliceosomes, ribosomes, tRNAs and the rest of it — needs to be present and in good working order. I think, however, that the deflationary connotations of ‘only’ do not do justice to the causal centrality of coding in protein synthesis.

As Bergstrom and Rosvall (2009, p.173) point out, the crucial difference between a world with a genetic code and a protein copying world is that the existence of an arbitrary genetic code is necessary to produce a freely combinatorial mapping between templates and products. And a freely combinatorial mapping is necessary to support the range of templates, and corresponding proteins, that make up complex biota.

Use of an arbitrary mapping turns the challenge of information transmission from one of passing on physical samples into a information-theoretic problem of how to package natural information for transport. In a world where proteins performed the function that molecular genes perform in this world, transmission fidelity would depend solely on the biochemical copying technology. There would be no scope for structuring redundancy, for arriving at assignments of representational token to content that minimise the consequences of copy error, or for conducting the other optimization activities of a communications engineer. In a DNA-based code, the chemically arbitrary assignments of codons to amino acids offer the degrees of freedom to do all of these things.

6.2 Are other developmental resources unlimited?

If the compositionality of the genome and the unlimited character of the genome as a developmental resource is one of the characteristics that allows it to harbor unlimited representational content, we should ask whether other developmental resources possess the same unlimitedness.

I will argue that genetic developmental resources are fine-grained difference makers — they make a multitude of very specific phenotypic differences — and that they are stable difference makers — they make the same differences over a reasonably wide variety of contexts. Other developmental resources do not display the same combination of attributes.

This is, at base, an empirical question. To start with a non-biological, pachinko-style, example. Suppose:

- o there is a hillside with a large number of rocky bollard-like protuberances scattered about on it;
- o at the top of the hill, at the entrance to the bollard zone, there is a single large bollard;
- o at the bottom of the hillside there is a line of bigger rocks with 100 crevices between them;
- o every so often a ball of dried dung bounces down the slope, subject to wind gusts, and enters the bollard zone;
- o if it hits the right hand side of the first big bollard, it is swept down a channel into the first crevice; if not, it bounces around among the little bollards, still subject to wind gusts, and ends up in one of the other 99 slots.

It is a contrived example, perhaps, but the parallel seems clear. All the natural information about which slot the ball ends up in is borne by the disposition of the protuberances, together with the timing, strength and direction of the wind gusts. The big bollard is just an on-off switch. If a ball strikes one side of it, it ends up in the first crevice. If not, which of the other 99 crevices it falls into has nothing to do with the big bollard; the wind and the little bollards do all the causal work. Here the large bollard is a limited contributor to the outcome. The wind and the little bollards add most of the richness to the library of possible outcomes.

Now consider a stylised genetic example. Suppose that:

- o we had an organism with 1,000 base pairs in its genome;
- o only one non-genomic factor influences the organism's ontogeny, the environment (E);
- o E has only two causally relevant states, E_1 , which allows the organism to grow to reproductive age, and E_2 , which causes the organism to die as a neonate;
- o there are 10,000 possible phenotypic outcomes, including early death.

One difference between the genetic factors and the environmental factor, then, is that the environment does not bear very much information. If E takes the value E_1 , there remain another 9,999 phenotypic outcomes that could arise. Which does arise is determined by the genetic

variables. If E takes the value E_2 , the organism dies as a neonate. Both the binary environmental variable and the multifarious genomic variables bear natural information about the phenotype but the genomic variables bear vastly more.

(I am assuming here that the causal relationships among the genomic and non-genomic variables are ‘stable’ in Woodward’s (2010) sense, i.e. that the causal regularities are reasonably counterfactually robust in the face of different background conditions.)

To generalise, consider all the different developmental resources that can affect the phenotypic outcome: DNA, cytoplasmic conditions, different dimensions of the environment, methylation patterns etc. Call them $C_1, C_2, \dots, C_n$. Suppose that each resource C_i has m_i possible states in the developmental process. Call the set of all possible states of C_i , c_i . Then the causal patterns are a function from the product set $S = c_1 \times c_2 \times c_3 \dots \times c_n$ to $O = [O_1, O_2, \dots, O_r]$, the set of all possible phenotypic outcomes. The whole function can be translated as:

(1) If allele a is at locus A and allele b' is at locus B and ..., and regions $X, Y, \dots$ and Z are methylated, and ..., and there was lots of iodine in the organism’s mother’s blood, and the nest in which the organism developed was warm, and ..., then the organism will have blue wing feathers and red body feathers.

(2) If ..., then

(3) If ..., then....

...

$(m_1 \times m_2 \times \dots \times m_n)$ If ..., then

Such a model extends the idea of ‘Mendel’s library’ (Dennett 1995, p.111) — the set of all possible genotypes — to include developmental resources internal to the organism that are not nucleic acid structures, and developmental resources in the external environment, as well as phenotypic characters. It is an empirical matter, but my claim is that most phenotypic variation described in the big function sketched above resides in heritable developmental resources, and particularly, in the genomic variables.

Now to address some worries.

First, the development function as I’ve sketched it uses discrete variable but clearly in real life some of the variables will be continuous, i.e. some members of the set of causal factors, or of outcomes, could take a value from the real numbers rather from a set of discrete options. For

example, in some species the average temperature at which the eggs are kept, a continuous variable, is a causal factor influencing the sex of the organism (Griffiths and Gray 1997, 476) and many traits, like height and weight, are continuous, not discrete. Resource variables like caloric intake can obviously be continuous as well.

This is true enough, but I do not think it really makes much of a difference. We could introduce continuous variables and my claim would just translate into a claim about how much one variable changes in response to a change in others and how stable the effect is.

Second, the patterns could be stochastic, not deterministic. Rather than a mapping from S , the set of sets of possible values of all developmental resources, to O , the set of possible phenotypic outcomes, we could construct the model as a mapping from S to O' , a set of probability distributions for each element of O . But again, this doesn't fundamentally change the pattern of relationships between developmental resources and phenotypic outcomes.

Third, the distinction between limited and unlimited heredity is very sensitive to how we individuate outcomes. In my stylised genetic example above, I identify only two states of the environment — a normal environment E_1 that allows survival and maturation of the organism and an unhelpful environment E_2 that brings about the death of the organism as a neonate. But different states of the environment might bring about the death of the neonate at different times. Why should we lump them all together into an omnibus E_2 ? On the other hand, why are we getting so fine-grained about phenotypic outcomes, distinguishing between eye colour and leg length and all the rest? Why do we not lump my 10,000 phenotypic outcomes together into two: P_1 (looking good for survival and reproduction) and P_2 (not looking so good)?

Well, the whole point of evolutionary biology is to explain the diversity of life on earth. We do not distinguish between slightly different points at which the neonate might die because that makes no difference to the processes of evolution and does not help us explain either the diversity of life on earth (or what might be represented at the sub-organismal level).

Finally, it could be argued that I am tacitly appealing here to a 'beanbag' model of inheritance that bears little relation to actual developmental systems, in which the influence of E_1 or E_2 will depend on what genome each co-exists with. This is really an empirical question. There are certainly examples where different environments make for predictably and importantly different phenotypic outcomes. For example, environmental sex determination arises in a range of organisms, including plants, nematodes, spoon worms, crustaceans, fish and amniote vertebrates like lizards, turtles and crocodiles (Janzen and Phillips 2006). And there are clearly important

cases, e.g. human language acquisition, where specific environmental inputs are necessary to ensure normal development.

So I am not claiming that all the instructions for ontogeny are in the DNA and all the other developmental resources are nothing but passive ‘backdrop’. I am, however, claiming that compared with the genome other developmental resources are less fine-grained and less stable difference makers.

There is no reason in principle why there could not be several mechanisms that generate unlimited variation. In my view, however, it just happens that there is only one other such mechanism, cultural inheritance. There are many other developmental resources around, some of which are passed down and modified from generation to generation — see section 7 below — but none of them generates unlimited variation.

This general empirical claim is equivalent to a set of claims about ‘norms of reaction’ where the level of expression of a particular phenotypic trait is given as a function of the organism’s genotype and its environment. So, for example, the adult height of a person could be modeled as a function of (a) particular aspects of their genetic makeup and (b) the nutrition they receive as they grow. For any particular genotype, a person’s height is determined by the nutrition they have received. Similarly, for any particular level of nutrition, a person’s height is just a function of their genotype.

It seems that in most cases, for any given genotype the phenotypic outcome is the same, at least over the majority of the environmental space; in other words, it is the genotype that makes the phenotypic difference, not the environment. Clearly that is not the case for every phenotypic trait in every organism; it is clear the story is much more complex in many cases. I am, however, claiming that the range of possible genotypes made possible by the compositionality of the genome’s structure means that DNA and other nucleic acid structures bear more, and more specific, natural information about organismal phenotype than do other developmental resources.

This is not to deny that an organism’s environment can exert quite fine-grained developmental control over its development and morphology, but in the vast majority of cases, it is only genes that are the *selectable* difference-makers. They do not exercise sole control over phenotypes, except perhaps in a few cases. But they are (with a relatively small class of exceptions which I will explore later) the controlling causes that are heritable and selectable. When we are working with a teleosemantic theory of representation, it is this that makes the genome the dominant inheritance system that underpins representation at the cellular level.

6.3 Arbitrariness

A natural question that arises at this point is what it is about the genome that underpins its enormous flexibility — its unlimitedness — as a developmental resource and inheritance mechanism.

One attribute that, at least intuitively, seems important is that the genome is in some sense symbolic. It is digital, not pictorial. Its elements can be assembled in any order. At least at the level of the genetic code itself, there is no necessary connection between the physical makeup of the codons and the amino acids for whose synthesis they act as a template.

This notion of arbitrariness seems important, both in the genome and in other representational systems like natural languages, mathematics, logic and computer code. But it is not immediately clear just what we might mean by arbitrariness and what it might contribute to the representational capacities of nucleic acid structures.

6.3.1 Arbitrariness in natural language

Arbitrariness, at least in the sense of the relationship between linguistic tokens and their representational content, is a commonplace in philosophy of language. In relation to nouns, the notion that the correspondence between a particular word and what it represents is arbitrary has a long and distinguished history in western philosophy. So, for example, Hermogenes in Plato's *Cratylus* (384d) says:

... no name belongs to any particular thing by nature, but only by the habit and custom of those who employ it and who established the usage.

Aristotle, in the *De Interpretatione* (1.2), says:

The limitation 'by convention' was introduced because nothing is by nature a noun or name—it is only so when it becomes a symbol ...

In *An Essay Concerning Human Understanding* (III.2.1), Locke says:

Thus we may conceive how words, ..., came to be made use of by men as the signs of their ideas; not by any natural connexion that there is between particular articulate sounds and certain ideas, for then there would be but one language amongst all men; but by a voluntary imposition, whereby such a word is made arbitrarily the mark of such an idea.

Hume (1739|1888, 490) says:

[L]anguages [are] gradually establish'd by human conventions without any explicit promise. In like manner do gold and silver become the common measures of exchange, and are esteem'd sufficient payment for what is of a hundred times their value.

In the continental tradition, Saussure (de Saussure 1966, p.67) points out that the linguistic sign — by which he means the combination of a signified, a concept like *SISTER*, and a signifier, the ‘mental image’ of a sound like *s-ö-r* (the sound of the French *sœur*) — is arbitrary in the sense that there is no ‘inner relationship’ between signified and signifier and the signified ‘could be represented equally by just any other sequence’.

Among more recent philosophers in the analytic tradition, Grice (1989), Lewis (2002) and others have also offered accounts of natural language that rely heavily on its conventionality.

This is not to suggest that all these philosophers have anything like the same theory of language or that they conceive of the arbitrariness of language in just the same way. For Saussure, for example, any relationship between the linguistic system and an independent external world is relatively unimportant and the structure of the system more arbitrary in that sense, while for more realistically inclined philosophers, the logical and conceptual structure of language is more closely constrained by the structure of the external world and so less arbitrary in the same sense. Nevertheless, it is common ground that the correspondences between basic semantic elements of a natural language — ‘horse’, ‘punch’, ‘eye’ etc. — and the bits of the world they represent are arbitrary in the sense that we could replace ‘horse’ with ‘porse’, ‘punch’ with ‘prunch’ and ‘mouse’ with ‘antimouse’ without loss or change of meaning.

So does the genetic code display the same kinds of arbitrariness as a natural language? We have hinted at one sense of arbitrariness, but how exactly should that be understood, and how, if at all, does the concept of arbitrariness translate to the genomic context? We will consider a number of alternatives.

6.3.2 The base sequence is free

First, we could mean no more than that there is no nomological constraint on the sequence of the bases in the DNA molecule (Monod 1971, p.106). This certainly appears to be true. We know of no law of chemistry that constrains the order of the bases.

This, however, is a relatively weak characterisation of arbitrariness and is not enough to guarantee that nucleic acid structures, if they bear representational content at all, do so by means

of an arbitrary, symbolic representational system. Imagine a representational system that represents the kinds of animals that die in a particular tar pit and the temporal order in which they die. Each kind of animal is represented by pictograph that looks like the animal seen side on. There's no constraint on the order in which the pictographs are recorded: no matter what order the animals die in, the string of pictographs is able to reflect that order, so the sequence is free in the current sense. And suppose, for the sake of argument, that it is the biological function of the pictographs to help some organism recover edible remains from the pit so that, on a teleosemantic view, the pictographs do bear representational content.

The fact that the atomic representational tokens of the system are tied to the shape of the animals that they represent denies them the arbitrariness that we see in natural languages and other fully symbolic representational systems. If a new kind of animal started dying in the pit, a new atomic pictograph that reflected its physical makeup would need to be formulated; it could not be composed out of existing elementary types.

It is also worth noting that other systems that clearly do not bear representational content do display this kind of arbitrariness. Consider the tree rings. There is no nomological constraint on the order in which broad and narrow rings appear; that is, the physical characteristics of the representing sub-system, the tree, impose no constraint on the order of the rings. Or consider layers of sediment on the bed of a river. A deep layer may convey the natural information that there were heavy rains in the catchment in the period during which the layer was laid down but the physical characteristics of the river may place no nomological constraint on the order of deep and shallow layers.

So it seems that the freedom of sequence in a linear representational system is a necessary but not a sufficient condition for a fully compositional representational system.

6.3.3 'Complexity merely suggests arbitrariness'

Godfrey-Smith and Sterelny (2007) suggest that the genetic code just *looks* arbitrary because the building of the protein is the end point of a long and complex causal process but note that a more detailed, molecular-level account of the process reveals a series of events completely consistent with the laws of chemistry.

Godfrey-Smith (2000, p.203) elaborates on the same idea when he suggests that the effect of a particular hormone in a particular biological context appears arbitrary because the hormone can have a wide range of effects depending on the context, that is, depending on the location and structure of the receptors with which it interacts. But he observes that the effects that the

hormone produces when it interacts with particular receptors in a particular context is determined by its physical structure, that is, a hormone with a different structure would produce different effects if it interacted with those receptors in that context.

All of this is surely right, but while the fact that the effects of a biological cause may vary widely depending on the context in which it operates may explain the appearance of arbitrariness in a particular process, it is clearly not capturing arbitrariness in the sort of linguistic sense described in the introduction to this section. Most long complex causal chains are obviously not arbitrary.

For example, the system of hormonal interactions that controls the oestrus cycle in many mammals is highly complicated and very finely balanced, yet the system as a whole, and the activation or suppression of one hormone by another within the system, are hardly arbitrary: it is an evolved system; it works repeatedly each cycle; it is essential to the reproduction of the relevant species; and the replacement of one hormone by another would entirely disrupt the operation of the system as a whole.

So even if we agree that the complexity and fine balances inherent in the synthesis of amino acids and proteins give process an appearance of arbitrariness, they do not confer arbitrariness on the code in any sense that parallels the arbitrariness of compositional representational systems.

We need something more.

6.3.4 History: a frozen accident?

Another way to approach the question stems from Crick's description of the genetic code as a 'frozen accident' (1968, p.369). Crick speculates that the genetic code we see today evolved in two stages. In the first stage, a few codon-amino acid assignments were established by chance (in some sense or other). Second, further assignments were established until the benefits of further expansion were outweighed by the costs. At this point the code became *fixed* because it determined the amino acid sequences of so many complex proteins that any mutation that changed the code would be fatal (unless accompanied by a vastly improbable number of simultaneous complementary mutations). What Crick (1968, p.370) says is:

In its extreme form, the theory implies that the allocation of codons to amino acids at this point [the point at which the code acquired its current structure] was entirely a matter of "chance".

In the current context, we could perhaps argue that arbitrariness, in the strong sense we are exploring means established by chance, in one sense or another. But in what sense?

We can hardly suppose that the molecular events that constituted the establishment of the code were uncaused. The same laws of physics and chemistry that hold today held three billion years ago and were obeyed by the code-establishing molecular events. Together with the initial conditions that obtained before the first assignments were established, we have no reason to doubt that those events were caused in the same sense, and in accordance with the same laws, as any other molecular events.

One slightly more plausible way of reading the claim that the genetic code was established by chance is that indeterminate quantum events played a decisive role in the establishment of the code. Of course, the genetic code is a molecular level phenomenon, and molecules are composed of atoms and atoms are composed of subatomic particles and some such particles display quantum indeterminacy. So quantum indeterminacy must have played a role in the establishment of the genetic code in the same weak sense in which it plays a role in the path a rock takes when it rolls down a hill or the development of a thunderstorm. That is not enough to make it the case that such macro-phenomena are chance events, or accidents.

By ‘played a decisive role’ above, I mean that particular quantum events — not large, statistically regular sets of such events — played a causal role in the establishment of the genetic code and that if alternative quantum events had occurred in place of those events, the genetic code would have been other than it is.

Now it is possible that quantum jumps may sometimes be responsible for point mutations in the genome. Löwdin has argued that:

occasionally a proton (hydrogen atom) could tunnel through one of the hydrogen bonds between two complementary base pairs in DNA. Since each of the canonical bases has a neutral charge, he argued that such a proton transfer would almost certainly cause a simultaneous anti-parallel proton transfer through another hydrogen bond in the base pair so as to keep the charges neutral. Since the bases are protected from the aqueous medium, the newly formed minor tautomers ... could sometimes be involved in DNA replication, causing mutations. (Stamos 2001, p.176)

Such ‘proton tunneling’ is a well-known phenomenon (Weihrich, Limage et al. 2004, p.147) but Löwdin’s conjecture remains no more than that. It depends on a popular but far from universally accepted model of the hydrogen bond and, while the conjecture is plausible, no empirical evidence of such proton tunneling in base pairs has yet emerged.

Even if proton tunneling occurs, and such indeterminate quantum events occasionally alter a biological outcome, it hardly seems likely that such events played a *decisive* role in the establishment of the genetic code. Vastly improbably collections of quantum events are, in

principle, capable of producing bizarre macroscopic outcomes — the pen hangs in the air rather than falling to the ground, the empty bottle becomes a rose in a gold cup, and so on (Omnes 1999, p.185) — but there is no reason to suppose that quantum indeterminacy influenced the fixing of the genetic code in any way different from the way it influences any other molecular level process (Graves, Horan et al. 1999, p.145). The probability that individual, or small numbers of, unusual quantum events — rather than the usual, vast, statistically regular collections of such events — played a decisive role in the molecular level processes that established the genetic code is Vanishingly small, as Dennett (1995, p.109) would put it.

Arguing that quantum indeterminacy has a significant role in DNA point mutations, Stamos (2001, p.179) notes that:

- o the thermal motion to which DNA polymerase is subject is widely considered to be partially responsible for DNA polymerase infidelity — that is, thermal motion can sometimes be strong enough to cause base pair mismatches;
- o the thermal motion acting on DNA polymerase is caused mainly by water molecules, since the environment of DNA polymerase is largely water;
- o since water molecules are small, their motion is affected by the quantum statistical nature of their electron orbitals;
- o there appears to be significant proton tunneling through the hydrogen bonds of some water polymers (Pugliano and Saykally 1992). While proton tunneling does not change the overall charge of a polymer, it does change its relative polarity and its interaction with other molecules.

Stamos thinks it is reasonable to conclude from these observations that quantum induced thermal motion on DNA polymerase is often the cause of base pair mismatches, but I think this may be a little ambitious. First, it is at least unclear that this is a reasonable conclusion. Stamos concedes that there are no quantitative models with which to estimate the prevalence of this phenomenon. Second, we have even less reason to be sure that this phenomenon was around 3 billion years ago when the genetic code was established.

While the empirical issue cannot be regarded as settled beyond doubt, it seems unlikely that indeterminate quantum events played a decisive role in the establishment of the genetic code.

I think a better way of reading the claim that the genetic code was established by chance, and one that links that claim naturally with a plausible account of arbitrariness, is to interpret ‘by chance’

(in evolutionary contexts) as meaning ‘through non-selective causes’ or, more permissively, ‘through non-selective causes or selective causes that depend on no more than local contingency’.

- o For example, if a species confined to a single island goes extinct because the island is entirely destroyed by a volcanic eruption, we would say that the species went extinct by chance, not by normal selective processes. I say ‘normal’ because, I suppose, in a very broad sense, catastrophic events like volcanic eruptions could be regarded as selective pressures but they are pressures that discriminate between organisms on the basis of only the grossest phenotypic traits — perhaps the cockroaches survive but all the mammals are wiped out.
- o An example of a selective cause that depends on no more than local contingency might arise if the volcanic eruption in the previous scenario does not destroy all the biota on the island but fills the environment with, say, silica. Organisms intolerant of silica succumb; others survive. This is clearly a selective process but one that depends on causal factors that are: local; highly unusual; and uncorrelated with the normal ecological web of interactions between hundreds or thousands of species and the non-biological environment.

Changes in the distribution and the phenotypic makeup of different species that arise in ways like this may reasonably be regarded as having been generated by chance — not in the sense of having no cause or being random in some fundamental sense, but in the sense of being caused outside the normal web of ecological interactions that drive evolution.

On this interpretation of chance, we can interpret Crick’s claim about the genetic code as saying that the existing code was established primarily through non-selective processes. Perhaps the assignments of codons to amino acids were entirely causally dependent on contingent local conditions. Or perhaps some of the first assignments were established through non-selective processes and selection between alternative codes accounts for only the later details of the existing code.

This captures some of the intuition behind Gould’s thought experiment that involves ‘replaying life’s tape’ (2000, p.48). As Beatty (2006) notes, there are two quite different ways of interpreting the claim that if you replayed life’s tape you would get a very different outcome from the actual outcome.

- o On a ‘causal dependency’ reading, an historical explanation of some biological phenomenon — for example, an explanation of the existing range of biota on this planet — rests on a sequence of antecedent states where any significant change in any step of the sequence would have altered the outcome. That is, the outcome of a process depends causally on the whole of the process. This seems right, but it does not really capture the notion of contingency that underlies Crick’s hypothesis (or, indeed, Gould’s thought experiment).
- o On an ‘unpredictability’ reading, an historical explanation of a biological phenomenon must appeal to factors other than natural selection. In Beatty’s words (2006, p.341), ‘[Gould] is denying that selection alone is sufficient to guarantee one particular outcome. Some other factors that distinguish the lineages or groups of lineages must be responsible.’
 - One other factor that I have already mentioned is non-biological causal factors: volcanic eruptions, floods, droughts, meteor strikes and the like.²⁹
 - A second factor is the order in which random mutations arise in a particular population. If mutation X arises first in a population, a phenotype with which it is associated may take hold and make it impossible for another mutation Y to prosper, even if organisms with Y are fitter than organisms with X in the context of the original population.
 - A third factor is genetic drift, which arises where some individual organisms in a population leave behind more offspring than others, not because of differences in fitness but just by chance (in the sense of causal factors uncorrelated with the attributes of the organisms involved). In small populations, drift can weed genes out of the population entirely, reducing its genetic diversity and making it more vulnerable to extinction (Wade 2008).

Since the genetic code was established around three billion years ago, it seems likely that we will never be sure about the role that chance played in its establishment. Nonetheless, the kind of ‘chance’ factors we have just noted do seem to make a fair degree of space for something like

²⁹ I should note in passing that these factors do not always produce unpredictable interventions in the normal course of evolutionary history. Floods are often entirely regular features of the environment, e.g. the Nile valley, and droughts form part of the ‘ecological backdrop’, e.g. the Australian bush.

Crick's hypothesis about the origin of the genetic code. Analysis of the code's chemistry will add further support.

6.3.5 Chemistry

We have so far looked at the arbitrariness of the genetic code from an historical perspective, asking how it was established and whether it could have developed very differently from the way it actually did. In doing that, we appealed to general considerations relating to contingency in evolutionary processes. We should also ask what chemistry tells us about the possibilities.

6.3.5.1 Other codes

We know that the standard genetic code is not the only nomologically possible code because we know it is not the only actual code. Some species display slightly divergent versions. For example:

- o In mitochondrial DNA, across all the major kingdoms, UGA specifies tryptophan rather than translation termination (Sarkar 1996, p.860).
- o Some species of yeast have ambiguous translation, so that, depending on the circumstances, CUG will act as a template for the synthesis of either serine or leucine (Knight, Freeland et al. 1999). In this case the mapping between base triplets and amino acids is not many-to-one but many-to-many.
- o Some species among both prokaryotes and eukaryotes have variations in the genetic code in which codons that usually specify translation termination specify particular amino acids. For example, in the bacterium *Mycoplasma capricolum*, UGA specifies tryptophan rather than the usual termination and in four species of ciliated protozoa, UAA and UAG specify glutamine rather than termination (Fox 1987).

Does variation of the genetic code between species or higher taxa, in itself, establish that the sequence of codons does not represent downstream structures? Sarkar (2000) suggests that such variations in the genetic code constitute evidence that information talk in molecular biology is no more than a potentially misleading metaphor. The claim appears to be that the genetic code, with variants in particular species, cannot form a single system bearing representational content because of the variant codings, or at least that the variants tell against the proposition that nucleic acid structures bear representational content.

I think both of these claims are highly implausible. We have no reason to believe that a system that admits of odd variations in its syntactic structure in different contexts is not a genuine representational system. To insist on complete uniformity risks denying that any naturally arising system is genuinely representational. Extensive variation in the syntax and morphology of natural languages hardly compromises their status as representational systems and similarly I do not believe that the presence of variation in the genetic code imperils its status as a representational system.

First, natural languages vary one from the other in phonemes, vocabulary, morphology and syntax. It seems natural to say that the usual genetic code and the variant codes in different species constitute different, though related, representational systems, just as related natural languages do.

Second, individual natural languages display considerable variation both synchronically and diachronically. Across time, natural languages evolve slowly (or quickly) and individual speakers employ unique idiolects that nonetheless allow them to communicate with others. Moreover, a particular dialect will often vary in some systematic fashion from a neighbouring dialect, for example, by substituting one phoneme for another or by way of some morphological shift.

Whether we consider the usual genetic code and its variants to constitute a group of historically related representational systems or a single system that admits of some variation, the variants of the code do not seem to provide any very strong argument against the proposition that the code and its variants are representational systems of some sort. Sarkar seems simply to be misguided on this issue.

It is also generally agreed that there is nothing in the chemistry of a particular amino acid that causes it to correspond to a particular base triplet. Monod (1971) puts it in these words: ‘there exists no direct steric relationship between the coding triplet and the coded amino acid ... this code ... seems to be chemically arbitrary, inasmuch as the transfer of information could just as well take place according to some other convention.’ So, for example, CAC codes for histidine but there is no chemical reason why it should not code for glycine (Maynard Smith 2000). Moreover, new types of base pairs, that are accepted by some polymerases can be designed and synthesised (Jablonka and Szathmary 1995, p.207).

6.3.5.2 Constraints and optimisation

While it is certain that there could be, because there are, genetic codes that differ from the standard code, this does not mean that the genetic code could be any way at all.

There are clearly some nomological constraints. Moreover, there is a considerable body of work that suggests that within the space of nomologically possible codes some are likely to be much more effective than others in underpinning evolutionary processes, and that the existing code is one of the more effective options available (Freeland and Hurst 1998). For example, there are some plausible chemical reasons why there are two base pairs in the genetic code, rather than three or one (which looks, *prima facie*, as though it would provide an economic and simple structure). One explanation relies on the properties of the secondary structures of molecules with one or three base pairs. Molecules with only one base pair collapse easily — they are unstable — and so would not be suitable to perform the functions of enzymes. Three-pair molecules, or at least random sequences of three base pairs, do not readily fold into stable secondary structures (Jablonka and Szathmary 1995, p.207).

We can also identify some features of the code that appear to boost fidelity of replication.

The code is ‘degenerate’ in the sense that there are 64 different base triplets and only 20 amino acids for which they act as templates. Three amino acids are specified by six different codons; five are specified by four different codons; one is specified by three different codons; nine are specified by two different codons and two are specified by a single codon. The code’s degeneracy displays some regularities which make it more stable than other possibilities. For example:

- o For each of the five amino acids that are specified by four codons, the first two bases are the same for each of the four codons and each of the four bases appears in the third position. The result is that a mutation in the third position will have no impact: the new codon will act as a template for the synthesis of the same amino acid as the original.
- o For each of the nine amino acids that are specified by two codons, the first two bases are the same for each of the two codons and either each of the pyrimidine bases (U and C) or each of the purine bases (A and G) appears in the third position.
- o In all known codes, if the first two bases of a codon are composed only of G and C, all four codons with those first two bases specify the same amino acid (Knight, Freeland et al. 2001, p.53). As with the first dot point, this structure ensures that mutations in the third base have no phenotypic impact.
- o If one of the first two bases is G or C and the other A or U, and the second base is a pyrimidine, all four possible codons specify the same amino acid. In some cases, however, CUG specifies serine rather than the usual leucine, creating an exception to this

regularity. If the second base is a purine, two of the four possible codons specify one amino acid and the other two, another.

Mathematical analysis of the structure and possible evolutionary trajectories of the code shows that it is extremely robust to translational misreading but there are also many more robust codes, which suggests that the standard code could indeed have evolved from a random code through a relatively small number of codon reassignments (Freeland and Hurst 1998), i.e., as Crick guessed, the standard code could be a combination of frozen accident with selection for error minimization. Once the code began to be established, even though it was not optimal, selection would have favoured conformity to the existing assignments.

In summary, then it remains an unresolved empirical question whether the regularities apparent in the actual dominant genetic code are symptomatic of significantly binding constraints on the code's structure, or whether they are simply contingent features that arose when the code was being established.

Clearly, the stronger the nomological constraints on the code are, the less we are entitled to regard it as arbitrary. In the extreme case, if the nomological constraints were so strong that the existing code were the only code that could support evolving biota, the code would certainly not be arbitrary. If there are some constraints on the chemical makeup of the code but there is still a very wide range of possible codes — and this seems likely to be the case — it seems reasonable to say that the code was established by accident.

The development of natural languages displays the same combination of chance (in the sense of non-selective causation) and nomological constraint. Many of the detailed features of a natural language are fixed by causal factors uncorrelated with the performance of the language's communicative function but not everything about a natural language is arbitrary. Human morphology and, if Chomsky is right, innate psychological constraints mean that the elements and structural principles of natural languages are not entirely arbitrary: there are some characteristics that they must possess if the language is to function effectively.

For example, natural languages are subject to constraints in the way phonemic 'features' such as voicing or voicelessness, vowel or stop can be composed into phonemes. For example, each phoneme must at least be capable of being formed reliably by the human vocal apparatus and apprehended reliably by our auditory system. And rules that adjust the features of phonemes have to trade off ease of articulation against ease of understanding.

- o Some rules aid the former, such as the ‘flapping rule’ under which, ‘if a stop consonant produced with the tip of the tongue appears between two vowels, the consonant is pronounced by flicking the tongue against the gum ridge, rather than keeping it there long enough for air pressure to build up’ (Pinker 1994, 175). Thus in many dialects of English, *patting* and *padding* are pronounced identically.
- o Other rules aid the latter. For example, English speakers round their lips when they say *sh* but not when they say *s*. Lip-rounding enhances the lower frequency noise that helps to distinguish between *sh* and *s*, making it easier for the listener to tell the two apart (Pinker 1994, 180).

Other constraints are apparently imposed by the limitations of the human brain. The capacities of our long term memory (and the need for rapid communication in real time), for instance, mean that lexemes have to be at most a few syllables long, not several hundred.³⁰ Gross features of human body structure also impose constraints. We have only mouth, one airway and one set of vocal cords, so we can produce sounds with only one stream of air.

We may conclude that the structure of tokens in the genome and in other representational systems are subject to some nomological constraints but that these are not so restrictive as to determine the way that content can be assigned to particular tokens. There is a good deal of space for both contingency and selective processes to contribute to the development of the natural languages and genetic codes that we observe around us.

6.3.5.3 *Chemistry and stereochemistry*

Finally, we should consider an argument from Stegmann (2004) that the nature of the process by which the codons in DNA act as a template for the synthesis of amino acids entails that the genetic code cannot be an arbitrary system. In particular, he argues that the code cannot be arbitrary because, while the relationship between a particular mRNA codon and the amino acid for which it acts as a template may be chemically arbitrary (as it appears to be), the processes of transcription and replication rely on complementarity between cytosine and guanine and between thymine and adenine. That is, transcription and translation could not occur unless (as is the case)

³⁰ Extremely long compound words can, of course, be composed of smaller units but these are not atomic semantic items.

cytosine and guanine, and thymine and adenine, fit together both ‘chemically’ — in terms of their covalent bonds — and ‘stereochemically’ — in terms of their three-dimensional structure.

For as long as arbitrariness is, in some way, essential for molecules to have meaning, we should expect that all molecules conveying meaning should be chemically arbitrary. They should be related arbitrarily to what is considered to be their meaning and to other molecules that are regarded as standing for them. (Stegmann 2004, 218)

So he thinks it may be possible for the relationship between a stretch of mRNA and a series of amino acids to be arbitrary but not for the relationship between (a) the DNA that acts as a template for the mRNA and (b) the amino acids.

I do not think this is right. If my characterisation of arbitrariness is correct, it is necessary only for one link in a causal chain to be arbitrary for chains including that link to ‘inherit’ the arbitrariness.

Suppose that:

- o Ada writes ‘the cat sat on the mat’ on a pad;
- o Berenice holds up in the window large placards with the same letters on them, and in the same order;
- o across the street in the telegraph office Cassandra, the sending telegraphist, taps out the Morse code corresponding to the letters on the placards; and
- o Diotima, the receiving telegraphist, transcribes the dots and dashes into letters on her pad.

The relationship between the letters on Ada’s pad and the letters on Berenice’s placards is not arbitrary: if Berenice held up a B whenever Ada wrote a C, the message would be distorted. (Of course, if some symbol other than ‘C’ were adopted by all four people, the message would still get through.)

Yet obviously Ada’s message and Berenice’s placards both convey the same representational content as the letters on Diotima’s pad. And that they do so relies on an arbitrary set of correspondences: another system could convey the same information, and indeed in our story another system, Morse code, does so. In the same way, transcription of a stretch of DNA into a stretch of mRNA must ensure that an A on the sense strand of the DNA molecule corresponds to an A on the mRNA, even though the codon in which the A appears is only arbitrarily related to

the amino acid for which it acts as a template. But the codon on the DNA still acts as a template for the amino acid.

6.3.6 Counterfactuals

So far we have been approaching arbitrariness in the genetic code by way of its history and its chemistry, exploring the combination of causal factors and nomological constraints that have shaped the code. Our conclusions have been that it is reasonable to call the code arbitrary if:

- o nomological constraints are not too strict: the laws of nature mean that there are many ways the code could have been and still supported evolving life; in particular, there are few or no nomological constraints on which codons act as templates for the synthesis of which amino acids;
- o selection among different possible codes may have played a role in the development of the existing code, but not too much;
- o causes uncorrelated with selective forces — i.e. ‘chance’ factors — played a significant role in the establishment of the code.

But there’s another account of arbitrariness we could consider based on the intuition that whether some feature of a system is arbitrary depends on whether particular changes could be made to it *now* without affecting the performance of its functions. Suppose you are working out how many tiles to buy to tile the floor of the bathroom. You might use a pen and paper to do some algebra in which you represent the number of tiles needed by ‘ x ’. We think this is arbitrary not because of the causal structure underpinning your choice of x rather than y , but because if you rubbed out x wherever it occurred and replaced it with y , you would still get the same answer and buy the right number of tiles.

On this kind of view, the causal history of the code’s establishment three billion years ago is not what makes it arbitrary; what matters is what is (in principle) possible now.

This, I think, is a view with some promise. Nomological possibility seems to be the sense of possibility that bears the closest parallels with natural language. Logical possibility admits a trivial parallel. It is clearly *logically* possible for the code to be replaced instantaneously by a different code but it is also logically possible that all the Japanese speakers could wake up tomorrow speaking Sanskrit instead of Japanese. This does not seem to capture what we mean when we say that the atomic semantics of a natural language is arbitrary.

If we consider nomological possibility it simply seems that it is no longer nomologically possible for the code to change, and this is quite close to our intuitions about natural language. It is certainly true that if Hannibal had wiped out the Romans in the Second Punic War, we would be using some other words instead of Latin derivatives like ‘servile’ or ‘puerile’, but this sort of historical contingency is only part of the story.

When we say that the relationship between word and object in a natural language is arbitrary we do not just mean that a given language could have developed differently to the way it has, we also mean that it could survive piecemeal reassignment of a different word to a particular object. For example:

- o if we all started saying ‘porse’ for ‘horse’ tomorrow, perhaps by order of a powerful and eccentric dictator, English would still work perfectly well. Horses would be watered and ridden and rendered into glue just as they are now. Only the signwriters and lexicographers would have extra work to do; or
- o if Emile suddenly and successfully changed his name to Jean-Paul, the mighty river of the French language would flow on undisturbed.

So this means that an arbitrary system displays a measure of modularity. You could, at least in principle, change one of its elements without having to change all of its elements.

On this view of arbitrariness, it is pretty clear that the genetic code is very much *less* arbitrary than any particular natural language. It is unlikely — but still possible according to the laws of nature (and even the laws of history, insofar as there are such things) — that we all start saying ‘porse’ instead of ‘horse’ tomorrow, but it is scarcely possible that, tomorrow, UCU could start to act as a template for tyrosine instead of serine. Too many molecular processes would be disrupted. This is just what Crick meant by a frozen accident and it constitutes a significant difference between the arbitrariness of natural languages and the arbitrariness of the genetic code. The degree of interdependence between the assignments of codons to amino acids seems much greater than that between the assignments of words to objects — or concepts, if you prefer — in natural language. As we have seen, this is not to say that just any sound capable of being produced by the human vocal apparatus could stand for any object but the degree of arbitrariness is much greater than for the genetic code.

6.3.6.1 *If you changed it, the code would still work*

The main distinction we have so far drawn between the arbitrariness of the genetic code and the arbitrariness of a natural language is that:

- o it appears logically, nomologically and historically possible for some semantically atomic element of a natural language to be replaced, now, with some other element and for the language as a whole to continue to function; but
- o it does not appear nomologically or historically possible for a particular assignment within the genetic code to be replaced now with another assignment without disrupting the functioning of the code as a whole.³¹

To take the analysis further we should try to be more precise about this distinction and the extent to which it holds. As a first attempt, let us suppose that there is a system *S* (like a language, or like the code), that consists of a set of types of entities (like words, objects, codons or amino acids) that possess particular properties and bear particular relations to one another. Then we might say:

- (6) a particular type of entity *E* in *S* (like the word ‘horse’, or the codon CCU) is arbitrary at time *t* in relation to *S* if a system *S'* that differs from *S* only in that *E* is replaced everywhere in the system with *E'* would function in the same way as *S*.

Arbitrariness is relative to a system because *E* may be arbitrary in relation to *S* but not to some other system *T* (for example, a crossword puzzle where, if ‘horse’ were replaced with ‘porse’, ‘porse’ would not perform the same functions as ‘horse’). Within the system there may also be some contexts that refer to the systems itself — i.e. where the representational system is representing some of its own features — where the substitution of ‘porse’ for ‘horse’ would change the truth value of some sentences. So, for example, ‘ “Horse” is spelled with an initial

³¹ By ‘historically’ possible, I mean something more restrictive than nomologically possible in the sense of ‘compatible with the laws of physics’. Given our current understanding of quantum mechanics, many occurrences are nomologically possible that would nonetheless appear impossible to all practical purposes. Historical possibility I will take to require compatibility with regularities in historically contingent systems like human history or evolutionary biology that are (a) instantiated over large samples, (b) have few or no exceptions and (c) display predictive power.

“h” is true in the normal version of English but “Porse” is spelled with an initial “h” is false in the porse version of English.

Formulation (6), however, only considers what would happen if E were replaced with E' , not whether this is possible or under what circumstances it might happen. It seems a bit odd to say that a system is arbitrary because of what we think would happen in quite impossible circumstances. To allow for this, we could expand the formulation to say that:

- (7) a particular type of entity E in S is arbitrary at time t in relation to S to the extent that:
 - (a) it is — logically, nomologically or historically — possible that a system S' that differs from S only in that E is replaced everywhere in the system with E' arise (or have arisen); and
 - (b) if S' arose (or had arisen), it would function (or would have functioned) in the same way as S .

In the context of the genetic code, this is tantamount to saying that the genetic code is arbitrary if it is possible that some other assignment of codons to amino acids could have arisen and underpinned natural selection in much the same way as the actual genetic code has. This is closer to a strong sense of arbitrariness that captures both the intuition behind Crick’s frozen accident theory and the analogy between the arbitrariness of the genetic code and the arbitrariness of features in natural language.

6.3.7 Conclusions

I think the story so far gives us reason for confidence that we can characterise arbitrariness in respectable terms — either by reference to causal history or current possibilities — and that the genetic code is arbitrary in the same sense that natural languages and other symbolic representational systems are.

So far as we currently know, a quite different genetic code could have supported evolved biota, perhaps with proteins composed of the same amino acids. The genetic code is arbitrary in a way that the relationship between the source and the receiver in most natural information systems is not.

Arbitrariness is important because it facilitates the compositionality that underpins the enormous richness — the unlimitedness — of the genome as a developmental resource and an inheritance mechanism.

It is also important to distinguish between two kinds of arbitrariness in the genome:

- o freedom in the arrangement of codons in DNA and RNA and in the corresponding amino acids in proteins — a weak sense of the term, though a crucial characteristic of the genome; and
- o arbitrariness in the correspondence between codons and the amino acids for whose synthesis they act as templates.

If we think that an mRNA represents the cellular conditions that it helps the cell deal with, then the fact that it is an mRNA made up of a string of particular bases in a particular order that does the representing is also arbitrary. *Given that* a particular mRNA corresponds to a particular protein product, it is not arbitrary that the mRNA represents that product: it is no accident that that product with its specific chemical properties helps the cell deal with the relevant conditions. But that's given the arbitrary correspondence between mRNA and protein.

The freedom in the order of the sequence of bases along the DNA and mRNA and the freedom in the sequence of amino acids along the length of a protein produce are both essential to ensure that there are an effectively unlimited number of possible proteins and possible interactions between proteins and nucleic acid structures.

These two forms of arbitrariness, then, are essential to unlimitedness but that is not so of the arbitrariness of the genetic code. Suppose we discovered that there were chemical constraints on the codon-amino acid correspondence that mean that it is nomologically impossible for the genetic code to be other than it is. Then the teleosemantic story about representational content in the genome would still go through. it would still be the function of the molecular gene to act as the template for the synthesis of a particular protein and it would still be the function of the ribosome to build a protein that corresponds to that template. Conversely, the presence of arbitrariness in a biological system clearly does not confer representational capacities on that system (Stegmann 2009).

It is suggestive and interesting that there are such close parallels between the arbitrariness of the genetic code and the arbitrariness of the correspondences between word and object in a natural language, both stemming from their historical evolution, but it doesn't seem to me that the

compositionality, and hence unlimitedness, of genetic representation rests on the arbitrariness of the genetic code.

6.4 Representing the counterfactual and the impossible

So far in this section we have been looking at the limits to the richness and power of the genomic representational system. Representation in the genome is largely pushmi-pullyu representation: the one token both reflects a state of affairs and prompts an appropriate response to it. I've argued that some forms of genomic representation are more sophisticated than this: for example, I think that the entrainment of molecular clock genes represents future events and that some genomic processes instigated by viruses and bacteria constitute deceptive representation. Nonetheless, representation in the genome seems closely tied to the actual: to states of affairs that are there right now and to specific (though not entirely inflexible) responses to them.

By comparison, natural languages seem a lot more freewheeling. As a matter of course we talk about things that didn't happen — the consequences if Athens had won the Peloponnesian War — and things that couldn't ever happen — what Aristophanes and Jonathan Swift would talk about over dinner. This makes some sense in a very flexible representational system. Different semantic units can be linked in complex inferential patterns to represent, or misrepresent, different states of affairs. Sometimes, in the process of inference, composing different semantic units gives rise to representations of states of affairs that simply cannot arise in reality. Now, since we have been looking at the limitations on the genome as a representational system, it seems natural to ask just how closely tied to the actual the genomic representational system is, and to what extent, if any, it is capable of representing counterfactual or impossible states of affairs.

6.4.1 Proteins

It is not at all clear that any proteins are impossible. There doesn't seem to be any chemical reason why any given sequence of amino acids could not be assembled into a protein. Amino acids in proteins are linked together by a 'peptide bond' between the carboxyl group of one amino acid and the amino group of the other. Because every amino acid has a carboxyl group at one end and an amino group at the other, each amino acid can join to any other (Berg, Tymoczko et al. 2002).

So it seems that any string of amino acids is chemically possible and there can therefore be no question of any nucleic acid structure representing an impossible protein.

We should also note here that the representation of proteins is limited to mRNAs and only a very small proportion of DNA sequences.

Many mRNAs have the function of acting as a template (or the precursor of a template) for the synthesis of a particular protein and so, on Millikan's formulation of representation (though not Shea's), are intentional icons for a particular protein.

The situation with DNA is, however, more complicated. Molecular genes in an organism's DNA have the potential, when expressed, to produce mRNA tokens with representational content but, even under Millikan's account of representation, only a small portion of an organism's DNA has this capacity.

Only some strings, the molecular genes, have been selected for acting as a template for the synthesis of a particular protein and under Millikan's teleosemantic account of representation they may be said to represent those proteins. Most of an organism's DNA — for example, 'junk DNA' or regulatory regions — have not been selected for acting as a template for protein synthesis and cannot therefore be said to represent a particular protein.³² So while any protein made up of amino acids is a chemical possibility and can be reflected in an appropriate DNA sequence, it seems that most DNA sequences do not represent proteins, even *in potentia*.

A key difference between molecular genes and sentences in natural languages is the more complex and flexible syntax of the latter. Molecular genes have been selected for their capacity to act as a template for the synthesis of a particular protein. While some sets of genes have co-evolved and work together in very complex bits of machinery, particularly regulatory machinery, they lack the hierarchical syntactical structures of natural language. It is almost as though each sentence of a natural language had been selected individually; as though 'here comes a tiger' means that a tiger is approaching because previous utterances of the sentence have helped other people survive and reproduce in the presence of tigers, not because the lexical and syntactical elements of the sentence have themselves been selected for their capacity to work together to represent a wide range of states of affairs.

³² 'Junk DNA' is a common term but we should note that it is generally applied to any DNA of whose function we are ignorant. Only about 2 per cent of human DNA is part of a molecular gene and much of the rest has no known function.

6.4.2 Traits

I have argued that, on a teleosemantic view of representation, a molecular gene or set of genes can be *for* a trait but that it cannot represent particular traits — basically because there is no single consumer device whose function it is to generate the trait. By the same reasoning, no set of genes can represent a collection of traits, or an entire organism.

But there is no reason why a set of genes cannot be *for* a combination of traits.

The gene *eyeless* in *Drosophila*, which we have met before, provides a helpful example. When *eyeless* is activated under Normal conditions, it results in the building of an eye in whichever compartment of the fly's body plan it happens to be located. If:

- o a *Drosophila* cDNA sequence capable of acting as a template for the synthesis of the Ey⁺ protein is placed under the control of a promoter for a heat-shock gene that is highly transcribed when temperature rises³³; and
- o the composite gene is inserted into the genome; and
- o the fly is then subjected to high temperatures;

the Ey⁺ protein is expressed in all cells. As a result, ectopic eye tissue can develop anywhere on the fly's body (Hartwell, Hood et al. 2000, p.712). It seems hard to doubt that it is the function of *eyeless* to bring about the development of an eye at a particular place on the fly's body. The same functional story applies to mammal eyes, under the control of the *Pax-6* gene (Lodish, Berk et al. 2008, p.29).

An appropriate set of molecular genes, then could be *for* a phenotype with eyes on each segment of the fly's body. This, however, cannot be in the sense that the set of genes as a whole has been selected for its ability to trigger the development of a fly with an eye on each body segment — clearly no such selective process has taken place. It can only be in the more limited sense that each gene in the set has been selected for its capacity to guide the development of an eye when it is expressed so that the set of genes taken one by one has the function of producing a fly with an eye on each segment.

³³ cDNA is DNA synthesised *in vitro* on an RNA template by reverse transcriptase. For promoter regions see section 2.2.6.

Not all genes can operate independently of others. The idea that they can, ‘beanbag genetics’, is now clearly inconsistent with the empirical evidence. So whether or not it is nomologically possible for each of a set of genes to be expressed independently of the others will depend on the particular case. This is an empirical matter. But in principle, it seems, it will sometimes be possible for independent expression to take place, and in such cases we can say the set of genes is *for* an unviable creature like the many-eyed fly.

If each of a set of molecular genes can be expressed independently, the genes have the same kind of compositional character as the elements of natural languages — they can be strung together in many different orders. This is what allows some sets of molecular genes to be *for* sets of traits.

Natural languages, though, have more flexibility than the genome. A speaker of a natural language can *represent* states of affairs that are not only non-actual but impossible, and represent states of affairs that are impossible in a number of different ways. For example, a speaker can say:

- o ‘my brother is a bachelor married to an engineer’, which is logically impossible; or
- o ‘my brother travelled faster than the speed of light’, which is nomologically impossible;
or
- o ‘my brother weighs fifteen tonnes’, which is biologically impossible; or
- o ‘my brother had tea with the emperor Nero’, which is historically impossible.

The best explanation is that basic (call them ‘Type 1s’) natural language utterances get their content from the way the world has to be (or become) in order for them to perform their proper functions. They are Millikan’s intentional icons. But other utterances (call them ‘Type 2s’) get their contents from the Type 1 elements out of which they are constructed (Zawidzki 2003).

This sort of construction is unavailable to molecular genes: they can only be *for* phenotypes, they cannot represent them.

6.4.3 The environment

So far we have been discussing whether molecular genes or mRNAs derived from them, can represent an impossible protein and whether they can represent (or be *for*) an impossible creature. Finally, we should also consider whether molecular genes or mRNAs can represent impossible states of affairs, either immediate chemical conditions in the cell or more remote conditions in the broader environment.

It is hard to see how a molecular gene or set of genes can *represent* an impossible state of affairs. I have argued that genes can represent states of affairs but they seem to lack the complex syntactical capacities of the elements of natural language.

According to the model I have been using here, a pushmi-pullyu token cannot represent an impossible state of affairs because the content of a token, if any state of affairs, is the state of affairs in which the token's ancestors have provoked responses in the consumer device that have conduced to the survival and reproduction of the consumer device (or of some larger system on which the consumer device depends). Such a state of affairs cannot be impossible because — while it does not need to have covaried with the production of the token perfectly, or even predominantly, over evolutionary history — it does need to have covaried with the production of the token to at least some extent and it must therefore be a possible state of affairs.

Zawidzki's suggestion, mentioned in the last section, makes it plausible that natural language utterances are capable of representing impossible states of affairs while molecular genes and mRNAs are not. We can see how the sentences of a natural language 'inherit' their content from the content of their elements, and these elements get their content from the functions of the mechanisms that generate them. So Millikan talks about (brain) mechanisms whose function it is to generate tokens (e.g. words or grammatical features) whose function it is to interact with other tokens (e.g. words or grammatical features) so as to perform various adapted functions (e.g. influencing the behaviour of the consumer device in a particular way).

6.5 Storage and decoupling

Finally, we should consider to what extent two other important features of some representational systems arise in the genome: the storage of representational content for later use and the decoupling of representational content from the responses to which it is its function to make a causal contribution.

Tokens of a natural language such as inscriptions or scratches on vinyl records or little bumps on DVDs (though not tokens such as the evanescent sound waves of speech) store representational content over time, so that it can be retrieved and consumed long after it is produced. Memories in the human head are an older example of representational content that is sometimes stored for long periods of time.

Are genomic representational tokens also stored in this way? The most obvious representational tokens in the genome are the mRNAs produced when a molecular gene is expressed. These aren't stored. They float around the cytoplasm until they strike a ribosome, when they are translated

into the amino acids of a protein. Once an mRNA gets to a ribosome, which it may never do, there's no mechanism for delaying the translation process. So there is no capacity for storage of mRNA tokens.

It might, however, be tempting to think of molecular genes in an organism's DNA as storing representational content.³⁴ After all, at least some (probably most) molecular genes in an organism's have the function of acting as a template for the synthesis of a particular protein under particular circumstances. We also know that most tokens of most molecular genes in DNA either:

- o are never expressed. They lie dormant until the cell dies and the DNA eventually degrades; or
- o lie dormant for a long period before being used to generate an mRNA that leads to the actual synthesis of a protein.

Still, it is still the function of a particular molecular gene in the DNA of a particular cell, as a member of its reproductively established family, to be expressed in particular cellular conditions. Provided the right producer-token-consumer functional structure obtains, a teleosemantic view can reasonably take the unexpressed molecular gene in the DNA as *potentially* representing either: the protein for whose synthesis it acts as a template (Millikan); or the conditions in which it is its function to elicit a particular adapted response from a consumer device (Millikan and Shea).

I do not believe, however, that a teleosemanticist can plausibly claim that an unexpressed molecular gene in the DNA *always* represents either its protein or its success conditions.

³⁴ It is particularly attractive to think about molecular genes in DNA as storing representations of phenotypes for later expression, in the particular organism or in its descendents. But, as I have argued in section 4.2 above, the teleosemantic view of representation makes it hard to accept this view. There is no doubt that at least some molecular genes in an organism's DNA bear natural information about that organism's descendents. In many cases, the presence or absence of a particular gene in an organism's DNA, changes the probability that the organism's descendents will display a particular phenotype. The problem, on a teleosemantic view, is that it is hard to identify a consumer device whose selective function it is to respond to those genes in subsequent generations by creating the relevant phenotype.

- o The DNA always corresponds, though not always in a straightforward fashion, to the final protein but under either Millikan or Shea's account of representation, the DNA has to be part of the producer mechanism and it is the token (or possibly the production of the token) that bears the representational content.
- o If the unexpressed molecular gene were taken as representing the success conditions for the expression of the gene, that would entail that during any period in which the gene is unexpressed and the conditions do not obtain, the gene is falsely representing the conditions as obtaining. That cannot be right. It is the function of many molecular genes (and their associated regulatory machinery) to respond to particular environmental circumstances when they arise, not to function all the time.

Consider the vervet. Even though we do not know all the biological details, it seems very likely that when there's no eagle about and the vervet is not uttering an eagle cry, there's some sort of pattern of neural pathways in the vervet's head that can be readily invoked to generate an eagle cry and so to represent (truly or falsely) the presence of an eagle in the vervet's vicinity. We could not very well say that the quiescent neuronal pathway represents the presence of an eagle — surely it doesn't do that until it is activated, but we can reasonably say that it potentially represents the presence of an eagle.

Similarly, if we think that an mRNA molecule represents the protein for whose synthesis it acts as a template (or the relevant state of affairs in the cellular environment), we should say that the relevant DNA molecular gene potentially represents the protein or the environmental state of affairs until its expression is triggered by the cell's regulatory machinery. We can then say that the mRNA bears representational content and the DNA, before the initiation of transcription, does so potentially.

Despite occasional suggestions in the literature (Stegmann 2005, p.425), it is difficult to see how the capacity of a producer device to harbour unexpressed representational tokens, or templates for producing them, bears on the question whether the genetic code bears representational content at all. Physical systems bearing natural information can also endure over time: tree rings bear natural information about the weather in past years, fossilised dung bears natural information about long-departed animals and strata in sedimentary rock bear natural information about floods or meteorite impacts millions of years ago. On a teleosemantic view of representation, it is the producer-token-consumer functional structure that gives rise to representational content, not the capacity of any of those three systems to persist over time.

It seems, then, that genomic tokens with representational content are not stored for later use, as are some tokens in more sophisticated representational systems. Storage, of course, is temporal separation between the production of a representational token and the generation of a response by the consumer device. In natural languages, writing and sound recordings insert a temporal gap between the production of the token and its reception by the consumer device. No such gap exists in genomic representation (at least, if I am right that we should not think of unexpressed molecular genes as bearing representational content). In natural languages — even if consumer, token and producer are all performing their proper functions — the response of the consumer device can come long after the consumer receives the token or, in the case of a purely indicative token, not at all.

For example, if one person tells another that, if a shark attacks, it can be driven away by punching it in the nose and the second person adds this to their store of beliefs, it is only in rare cases that the second person *ever* acts on their new belief. And in almost no cases — only if they are actually getting attacked at the time — do they act on their new belief as soon as the token is received.

In the case where an mRNA is representing the protein for which it acts as a template, there is no comparable decoupling of token, reception by the consumer and the consumer's response. The mechanics of transcription and translation ensure that it is the function of the consumer device to translate the mRNA into amino acids as soon as it reaches the ribosome. However, in the case where mRNAs are representing environmental conditions — i.e. the evolutionary success conditions associated with the response from the consumer device — the circadian clock examples (see section 5.1) show that the response of the consumer device can be temporally decoupled from the production of individual tokens. The decoupling is not flexible, as it is in natural languages. It is the function of the consumer to generate a particular response at a particular future time and that response is not determined by interaction with other representational tokens; so there is no inference going on, and no interaction between indicative and imperative tokens.

6.6 Conclusions

In this section we have identified some features of representation in the genome that make it a powerful representational system and others that limit what it can represent and the ways its representations can be used.

The compositionality of the genetic code and the huge number of different tokens that can be assembled from the small number of bases that make up nucleic acids, give the genome effectively an unlimited number of mRNAs and tokens to work with. The arbitrariness of the genetic code — in the sense that any order of bases, and any protein composed of the 20 usual amino acids is chemically possible — underpins the code's compositionality. The code is almost certainly arbitrary in another sense — that the set of correspondences that actually holds between codons in DNA, codons in mRNA and amino acids in proteins could have been entirely different from the way it is. It appears, however, that arbitrariness in this sense, while presenting intriguing similarities with natural languages, does not in itself add to the representational power of tokens generated by the genome.

Genomic representation is also tied more closely to representation of the actual and immediate than more sophisticated representational systems. Nucleic acid structures cannot represent impossible proteins, simply because there are no nomologically impossible proteins: amino acid chemistry guarantees that any protein composed of the usual amino acids is possible, though of course only a tiny proportion of all possible proteins occur in nature. The picture is a little different with the representation of traits. The functional structure of teleosemantic accounts of representation mean that no nucleic acid structure or set of nucleic acid structures is able to represent an impossible or counterfactual trait, though it may be able to be *for* a trait — a considerably weaker notion). In relation to representation of the environment, whether immediate and internal to the cell or the broader external environment, the functional structure of teleosemantics again makes it impossible for nucleic acid structures to represent impossible states of affairs.

Finally, there is only limited decoupling of genomic representation and behavioural response. The genetic clock examples I discuss in section 5.1 involve a temporal separation of the production and consumption of a representational token but for the most part it seems that genomic representations are much more closely tied to the consumer device's response than the representations of more sophisticated systems.

7 Too much representation?

So far we have outlined a range of teleosemantic theories of representation, based on an aetiological view of biological function. We have then asked whether, under such theories, at least some nucleic acid structures have representational capacities and we have looked at a number of kinds of things that nucleic acid structures may be capable of representing. We have also explored some of the factors that add to and detract from the power of the genome as a representational system. One question that seems to arise naturally at this point concerns the consequences of this account of representation for our view about the prevalence of representation in the biological world as a whole.

Remember that our teleosemantic account of representation holds that representational content is derived from the biological functions of the entities involved and that these functions are derived from the selective history of the entities. Since we know that many molecular genes and regulatory regions in DNA have been selected for over evolutionary time it comes as no surprise that they have functions based on their selective histories. It turns out, too, that at least some of these nucleic acid structures participate in the kind of functional structures that, on a teleosemantic of representation, confer on them representational content.

But we might ask, are there any selective processes *other than genetic selection* that also underpin aetiological functions and, if there are, are those functions so arranged as to generate representation of the kind we have been discussing?

The question seems particularly pertinent in light of the extended debate about whether genes — construed in one way or another — hold a special status among all the developmental resources that are necessary for the development of a viable organism and whether they have a unique role in intergenerational inheritance. There are many ways of claiming that genes do have some special status (Stegmann 2012).

One fairly common claim is that only nucleic acid structures are biological replicators, i.e. (roughly speaking) items that are directly copied from one generation — not necessarily an organismal generation — to the next and that pass changes in their structure on to the next generation (Hull and Wilkins 2008).

There are clearly a number of developmental resources other than nucleic acid structures that are passed down from generation to generation: we will be discussing a number of them later in this section. For example, in sexually reproducing organisms almost all of the zygote is inherited from the mother. This includes enzymes, organelles and other important developmental

resources. But it is much less certain that changes in the structure of these inherited developmental resources are also passed down from generation to generation, so it is possible to argue that molecular genes are nonetheless the only replicators.

A more specific way of privileging genes over other developmental resources is to claim that genes carry information (of some kind) in a way that other developmental resources do not. There is no doubt that many biologists think that genes carry information about the phenotype of the adult organism in a way that no other developmental resource does — see the quotes in section 1.2. That is the kind of claim that I am defending in this section. I think it is quite clear that developmental resources other than nucleic acid structures convey natural information but I will argue that, under a teleosemantic view of representation, nucleic acid structures are the only developmental resource (other than cultural resources) that undoubtedly bears representational content. That is not to say that it is impossible for other developmental resources to do so as well but in this section I will argue that as a matter of fact it is only nucleic acid structures that certainly do so and that the most we can say of other developmental resources is that in some cases they might do so.

To make this plausible, we need to find a principled difference between nucleic acid structures and the other developmental resources that might be considered to bear representational content.

Remember that, in broad terms, our teleosemantic story holds that:

- o if a biological physical token is to bear representational content, it must be generated by a producer device — which will often be some kind of developmental resource — that participates in a particular producer-token-consumer functional structure; and
- o if a developmental resource is to possess a biological function Z, it must have been selected for doing Z; and
- o if a developmental resource is to be selected for doing Z, particular conditions — roughly speaking, variation, heritability and differential fitness — must obtain.

I will argue that every developmental resource that might be thought to bear representational content on a teleosemantic view of representation in fact fails to meet at least one of these conditions.

In most cases I will argue that while an inherited developmental resource may have a biological function, it will not be the right kind of function to underpin teleosemantic representation. But in

some cases, it is questionable whether the developmental resource has undergone selection at all, i.e. it is questionable whether the third condition above has been met.

We have already discussed in some detail the requirements for representation on a teleosemantic view and the notion of biological function that underlies representation, but we have not discussed what is needed for natural selection. Since on our teleosemantic account of representation, natural selection is necessary for the establishment of any biological function, and since I will be arguing that a number of non-genomic developmental resources have not undergone natural selection, we should try to get at least fairly clear about what it is.

7.1 Conditions for selection

The conditions for selection among a set of items in a single generation are relatively thin. All you need is a set of items of at least two types and some causal mechanism — sunlight, moonlight, cold, heat, a cloud of volcanic dust, a bacterium, a predator — that destroys one of the types less readily than the others in a counterfactually robust fashion. We may say that that type has been selected for in that generation. But in most cases, the causal history of one generation will not go very far in explaining why one trait is common and another rare.

In the multi-generation case, however, it is no easy task to give necessary and sufficient conditions for the occurrence of natural selection. Most of the summaries in the literature involve more or less tacit idealisations of real world populations and processes. Still, we have to give some indication of what is needed for natural selection, and therefore biological function, to arise. At the least, we need what Godfrey-Smith (2009, p.39) calls a *Darwinian population in the minimal sense*, that is:

a collection of causally connected individual things in which there is variation in character, which leads to differences in reproductive output (differences in how much or how quickly individuals reproduce), and which is inherited to some extent. Inheritance is understood as similarity between parent and offspring, due to the causal role of the parents.

This is a broader notion than the recipes for natural selection given elsewhere in the literature, e.g. by Lewontin (1970, p.1), Szathmáry and Maynard Smith (1997, p.559) and Ridley (1996, p.70). Godfrey-Smith does not purport to give sufficient conditions for evolution by natural selection: in particular, a population can be a minimal Darwinian population without the appearance of new characters. But we can, I think, take it that we need at least a minimal Darwinian population if natural selection is to operate.

7.2 DNA and other developmental resources

Obviously DNA and associated nucleic acid structures are developmental resources that are selected for in actual biota.

- o Molecular genes are generally copied accurately from parent to offspring. In asexually reproducing organisms — if the parent has a particular allele at a particular locus, the offspring will usually have that allele at that locus. In sexually reproducing organisms — the offspring will inherit one of each pair of alleles from each parent.
- o Changes in germ line DNA sometimes give rise to a new phenotype in the offspring. These changes, along with the new phenotype, are passed on to succeeding generations of organisms.
- o The different phenotypic traits arising through mutation very often, though not always, have different effects on the fitness of the organisms that bear them.

But are other developmental resources selected for as well?

There is no a priori reason why the genome has to be the only inherited developmental resource capable of participating in natural selection (Mameli 2004; Shea 2007, p.321). So, for example, Jablonka and Lamb (2005, p.117) imagine the planet Jaynus, colonised by one earth organism millions of years ago. Jaynus is now inhabited by wide range of organisms with different structures and different cell types but no differences in DNA. All mutations in DNA are ruthlessly weeded out but inherited changes in phenotype can still arise because of random variation in epigenetic inheritance mechanisms. As a result the range of organisms on Jaynus is comparable in diversity to the range of organisms on earth, despite their identical DNA. There is nothing logically impossible about the scenario and nothing obviously contrary to the laws of physics or chemistry.

Moreover, there are some inherited developmental resources that, at least at first blush, might give us cause to doubt that the genome is the only inherited developmental resource capable of underpinning representational functions. These include:

- (1) methylation patterns;
- (2) symbiosis;
- (3) niche construction;

- (4) hormonally mediated inheritance;
- (5) cellular membranes;
- (6) the inheritance of characteristics acquired from the extra-organismal environment;
- (7) cortical inheritance; and
- (8) prions.

Each of these will be discussed in the following sections.

7.3 Methylation patterns

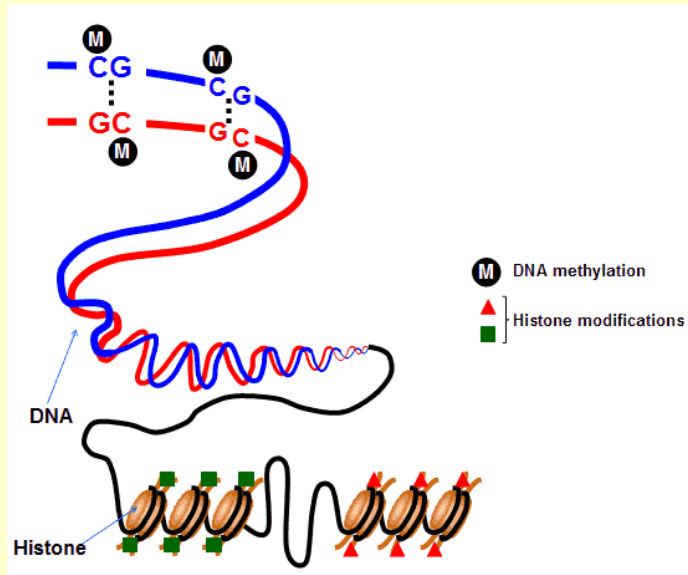
Methylation patterns, in which methyl groups are chemically associated with particular DNA sequences, are an inherited developmental resource that can have very significant phenotypic effects. Do particular methylation patterns have biological functions and, if so, do they bear representational content on a teleosemantic view of representation.

7.3.1 Biology

Each chromosome in a eukaryotic cell contains one very long DNA molecule, up to 2.8×10^8 base pairs in length. The length of the DNA is up to 100,000 times the cell's diameter, so the packing of DNA is essential to its effective replication. DNA is packaged in a complex called chromatin, in which the DNA molecule is wound around cores composed of proteins called histones — there are five different types. The basic unit of chromatin is the nucleosome, composed of 146 base pairs of DNA, a little less than two full turns of the double helix, and eight histones. A string of nucleosomes is twisted into a chromatin fibre. Each of the histones has a flexible tail of between 19 and 39 amino acid residues (Lodish, Berk et al. 2008, p247). The tails may be subject to a number of modifications after the histones are assembled at the ribosome. An acetyl group may be attached to lysine residues in the tail ('acetylation'). Or a methyl group may be attached to a tail ('methylation'), usually to cytosine (Jablonka and Lamb 2005, p.130).

Figure 12 illustrates the structure of chromatin.

Figure 12: Methylation and histone modifications



Source: Extremelongevity.net, <http://extremelongevity.net/2011/10/27/is-dna-methylation-a-reversible-cause-of-aging/>, accessed 14 July 2013.

The methylation pattern of a cell is replicated in all the cells descended from it. Methylation patterns can be passed by the parent organism to the offspring's DNA in a sperm or egg. For example, it has been proposed that female humans methylate a particular sequence on the X-chromosome in their eggs so that males, who get their only X-chromosome from their mother, cannot transcribe that region. Males demethylate that region in their sperm so that female offspring are able to transcribe the region on the X-chromosomes they receive from their fathers. The region may have a negative phenotypic effect on aggressiveness (Griffiths 2001, p.400).

Methylation is very common in eukaryotes but does not occur in all species, for example, not in *S. cerevisiae* (brewer's yeast) or *C. elegans* (a roundworm) and probably not in *Drosophila* (the fruit fly). Nonetheless, its wide distribution indicates that it is a very old phenomenon, probably predating the emergence of eukaryotes.

We do not know what the function of methylation is in all cases. We do know that it often inhibits the initiation of transcription so that, in most cases, methylated genes are not transcribed (Colot and Rossignol 1999, p.406). This is the case in vertebrates but is not universal — in fungi, for example, methylation of promoter regions does not impair gene expression.

Parental imprinting is a particular kind of chromatin marking. In mammals, a particular chromosome or molecular gene may be differently methylated depending on which parent it came from. Sometimes only the gene from the father is active and sometimes only the gene from the mother. So if a gene is subject to parental imprinting, two individuals with identical DNA,

both with one normal and one faulty allele may have quite different phenotypes, depending on whether they acquired the faulty allele from the father or the mother (Jablonka and Lamb 2005, p.254).

For example, the mouse *Igf2* molecular gene is expressed only if it was inherited from the father; a copy inherited from the mother is not expressed. Conversely, the mouse *H19* gene is expressed only if it was inherited from the mother. The consequence is that imprinted genes are expressed as if only one allele were present, even though there are two copies of each of these molecular genes in each cell. Furthermore, when these genes are examined at the molecular level, no changes in their DNA sequences are observed; the only changes that are seen are extra methyl groups present on certain bases of the DNA of the imprinted genes (Griffiths, Miller et al. 2000, §11).

The gist is that, somehow, a piece of a chromosome can be labeled as different on the basis of its ancestry or on the basis of which other genes were in the same genome. In many cases, differences in DNA methylation are associated with differences in molecular gene activity. It certainly appears that one function of methylation is the regulation of molecular gene activity but the underlying mechanisms and an explanation for its evolution remain elusive.

7.3.2 Do methylation patterns bear representational content?

Against this biological background, we now need to ask whether methylation patterns bear representational content.

To begin with, we know that methylation patterns are an inherited developmental resource:

- o Methylation patterns are passed down from generation to generation.
- o They are passed down reliably, with high fidelity.
- o De novo methylation occurs, so that fidelity is not absolute, and the new pattern is then copied to subsequent generations.
- o The different methylation patterns cause the development of different phenotypes by controlling which genes are switched on or off.
- o Methylation does not affect the sequence of bases in a cell's DNA.

This does not, however, entail that they are an independent inheritance mechanism.

First, the proteins that accomplish methylation are themselves the products of synthesis at the ribosome on the template of codons in the organism's DNA. We do not know for sure but it seems reasonable to suppose that the molecular genes that act as templates for the proteins that methylate and demethylate DNA have themselves been selected for the proteins' methylating and demethylating abilities.

Second, the phenotypic effects of methylation are entirely mediated through DNA. In the causal chain — or the web of causal chains — that connects a methylated or unmethylated stretch of DNA to some phenotypic trait, it is only through the expression or non-expression of the stretch of DNA that methylation makes a causal contribution. Methylation influences which DNA sequences are expressed but that seems to be as far as it goes: it functions like the censor's black marker pen, redacting some bits of text and leaving others to convey their content to the consumer. It is clearly an important feature in the regulation of gene expression, but it participates in communicating representational content only as part of the genomic representational system.

7.4 Symbionts

In many species, communities of symbionts — often bacteria or protists — that live within the body of a host organism are essential to the host's chances of survival and reproduction.

The function of most such symbionts is to aid in the digestion of food. This is the case in many species of insects and other arthropods (Cazemier, Hackstein et al. 1997, p.194) and in mammals as well (Hooper, Midtvedt et al. 2002). For example, the Western flower thrips (*Frankliniella occidentalis*) is a plant eating insect that occurs all over the world. It has a permanent association with bacteria of the genus *Erwinia*, which are passed from generation to generation via the plant food source.

The means by which the host organism acquires its symbionts varies from case to case.

- o Young mammals do not acquire their symbiotic gut flora directly from either parent. They are sterile as foetuses and pick up the flora when they pass down the birth canal.
- o In other cases symbionts are passed directly from parent to offspring, rather than picked up by each new generation from the extra-organismal environment. For example, vertical transmission may occur through coprophagy (Dillon and Dillon 2004, p.84). Larvae of the cockroach (*Eulaberus posticus*) acquire gut bacteria by eating their mother's faeces and recruit more bacteria after each moult by eating their own faeces (Cruden and

Markovetz 1984, p.134). Some ungulates and other herbivores also rely on symbionts, acquired by coprophagy, in order to be able to digest their customary diets (Troyer 1984).

- o Lice require bacterial symbionts to supplement their normal diet of vertebrate blood. The symbionts live inside host cells ('mycetocytes'), which clump together into a 'mycetome' that, at a particular point in the louse's life cycle, infects special organs in the female next to the ovaries, the 'ovariole ampullae'. For example, in the genus *Pediculus*, which includes the common lice that infest humans, the symbiotic bacteria gather at the ampulla at the time of the third larval moult and from there transfer to depressions in the egg cells — between 150 and 250 per cell — which then close behind them (Frank 1996, p.1116).³⁵
- o Transfer of bacterial symbionts via the gametes from the female parent occurs in a number of other bacteriocyte-insect symbioses (Xu and Gordon 2003). For example, in three insect groups — Dictyoptera (cockroaches), Homoptera (aphids, cicadas, scale insects etc.) and Coleoptera (beetles, weevils etc.) — mycetocytes allow the transmission of symbionts via the egg cells (Douglas 1989).

Further, in some cases, presence of particular symbionts is necessary for the expression of particular molecular genes in the host.

- o In the Hawaiian squid *Euprymna scolopes*, the luminescent bacterium *Vibrio fischeri* is needed for the expression of particular genes that are necessary for the development of the squid's light organ (Visick and Mcfall-Ngai 2000, p.1779). The organs of young squid include ciliated epithelial cells that aid in harvesting *V. fischeri* from surrounding seawater. The bacteria destroy the ciliated cells soon afterwards by excreting a particular protein that promotes differentiation of light organ epithelial cells, radically changing the size and shape of the organ. The organs of squid that are not exposed to *V. fischeri* remain undeveloped.

³⁵ Moulting of feathers occurs in birds, of the skin in snakes and of fur in mammals. In arthropods moulting, or ecdysis, is the shedding of the exoskeleton as a whole. Larval moulting is a repeated phenomenon in insect development when the insect sheds its exoskeleton to allow for further internal growth. The number of moults in the life cycle varies widely from species to species.

- o Which bacteria are in the diet of *Drosophila* affects the expression of the *dipt-lacZ* reporter (molecular) gene. Feeding the protozoan *Crithidia bombi* to *Drosophila* induces synthesis of a number of antimicrobial peptides in the haemolymph (Dillon and Dillon 2004, p.85).³⁶
- o There is now strong evidence that symbiotic microflora, especially in the gut, are necessary for the normal development of the immune system in mammals, including humans. Germ-free mice lack normal immune responses to ovalbumin while normal responses are restored if a single component of the usual microflora is introduced into the gut of newborns (Hooper and Gordon 2001).
- o Colonisation of germ-free mice with *Bacteroides thetaiotaomicron* affects expression of mouse genes that regulate maturation, nutrient uptake and metabolism, and the growth of new blood vessels. Germ-free mice must consume 30 per cent more kilojoules to sustain their body weight than animals with the usual microflora (Hooper, Wong et al. 2001).³⁷

So, if symbionts are essential to gene expression in the host and communities of them are reproduced, one way or another, from generation to generation, they (together with the mechanism by which they are passed from generation to generation) are an inherited developmental resource, not just part of the ecological backdrop.

However, if populations of symbionts and the mechanisms by which they are passed on are to possess biological functions — and *a fortiori* representational functions — they must undergo selection. So do populations of symbionts vary from generation to generation in ways that are passed on and that make a difference to the survival and reproductive success of the host or the symbionts?

In some cases the relationship between host and symbiont is exceedingly intimate. The symbiont is essential (‘obligate’) for the survival and reproduction of the host and vice versa. Moreover, bacterial symbionts often co-evolve with the host species (Dillon and Dillon 2004, p.83). This is

³⁶ Haemolymph is insect blood. The parallel with mammalian blood is, however, only approximate: the circulatory system of insects differs from that of vertebrates (and many invertebrates) in that the haemolymph is confined to vessels only some of the time. The rest of the time it circulates ‘in the open’ within the insect’s body cavity (the ‘haemocoel’).

³⁷ Villi are small, projecting blood vessels on the lining of the small intestine.

more common among insect symbionts that live within host cells ('endocellular symbionts') but some cases have been identified even among extracellular ones symbionts, for example, gut symbiotic bacteria of some stinkbugs (Kikuchi, Hosokawa et al. 2009).

Horizontal transfers of symbionts from host to host represent a mechanism for generating phenotypic variation in the symbiont population. In some cases, the introduction of a new symbiont will be harmful to the host organism so that both the host and its symbiont population will be less likely to survive and reproduce. In some cases, the introduction of a new symbiotic species will be good for the host and this host-symbiont phenotype will increase in frequency with in the population of hosts.

We also know that a number of host species have mechanisms that reduce genetic variation or competition in symbiont populations, thus maintaining their contribution to the host's metabolism and preventing them from becoming virulent. In these cases, there is sometimes active control of symbiont populations by the host organism, analogous to DNA error correction (Frank 1996).

- o There is often a tradeoff for the symbionts between being successful and becoming so virulent that they compromise the viability of the host and damage their own prospects.
- o The balance between virulence and reproductive success depends on how much genetic variation there is in the whole symbiont population and how much in different lineages within that population: less relatedness means more competition within the symbiont population and more virulence.
- o As a consequence of this dynamic, host traits that favour more relatedness among the symbionts passed on to the next generation are selected for because they tend to reduce virulence.

This kind of example shows that the makeup of symbiont populations is a phenotype subject to selective pressure both from the external environment and from the internal biology of the host. Changes to the makeup of a symbiont population or, more drastically, failure of transmission of symbiont populations, can have important impacts on the fitness of the host organism as well as the symbionts themselves.

We may conclude, then, that symbiosis constitutes a developmental resource that is replicated from generation to generation of the host organism. In addition, symbiont populations can vary from generation to generation and variations can affect the fitness of the host organism and the symbiont population.

Nonetheless, while it seems reasonable to conclude that some symbiont populations undergo selection and possess biological functions, there are reasons to doubt that they have the kind of functions that could underpin representation.

First, the mode of transmission of symbiotic relationships, based on a sample of the symbiont species in either the previous host generation or in the broader environment, limits the scope for symbiont transmission on its own to underpin a selective process. Sterelny (2005) draws a fundamental distinction between sample-based and information-based inheritance mechanisms. He points out that there is no arbitrary coding involved in symbiotic inheritance mechanisms. So, for instance, a termite acquires the bacteria that will digest cellulose in its gut directly from the anal secretions of its nest mates. It adopts a sample of the microflora from which the full complement grows. Even when a symbiont is transmitted from generation to generation of the host species by stowing away in the host oocytes, like the lice symbionts described above, the population in the next generation is derived from a sample of the population in the last.³⁸ This limits the scope of variation that can arise in transmission from generation to generation: by contrast, the compositional character of genomic inheritance means that a single mutation can have wide ranging phenotypic impacts.

Second, it is hard to see what would fill the producer, token, consumer and response roles in the case of symbiosis. A population of symbionts can obviously make a crucial contribution to the survival and reproduction of its host but it does not look as if it participates in the kind of functional structure that our teleosemantic account of representation requires. There is reason to believe that symbionts have biological functions — probably via gene selection (see next paragraph) — but not that they have representational functions.

Third, we can attribute a biological function to a population of symbionts but not, so far as we know, because heritable variants in the size or composition of populations, generated otherwise than by genetic inheritance and variability, have fought it out in terms of fitness. The selective mechanism, rather, has been the genotypes of the host and symbiont, selected for their capacity

³⁸ We should note in passing that it may be putting things too baldly to say that there is no flow of information between one generation of symbionts and the next. Since the occurrence of a population of a particular symbiont species in one organism (the receiver) reduces the uncertainty attending whether a population of the same species occurred in the organism's parents (the source), we can be confident that at least natural information is being passed on. But if populations of symbionts are to generate representational content, symbiont transmission needs to do more than this.

to live together successfully. The qualification ‘so far as we know’ is necessary: it certainly seems nomologically possible that variation could arise in the makeup of the symbiont population through some non-genomic variation-generating mechanism and the different ‘phenotypes’ thus generated could be subject to selection.

7.5 Niche construction

As we have seen, DNA carries natural information about the organism’s phenotype. Some phenotypes confer a higher degree of fitness on the organisms that display them than others, given the environment in which the organisms find themselves. These organisms and the genes they carry reproduce more than organisms with low-fitness genes and phenotypes. Populations of organisms tend over time to acquire more high fitness phenotypes and more of the genes that give rise to them.

This is just a crude model of gene selection, but the important point for present purposes is that it takes the environment as given: genes and organisms are selected by how well they deal with a given environment.

What if the environment is not independent of the organism?

This is certainly true in a weak sense: all living things maintain an energetic disequilibrium between an internal and external environment (Turner 2004, p.330).

It also seems reasonable to suppose that almost all species at least sometimes modify their environments in a way that affects the fitness of their members. Even so modest a modification the environment as defecating in it can affect an organism’s chances of survival and reproduction, by affording clues to predators or prospective mates, or providing a means of diffusion for dangerous parasites.

There are also more intimate relationships. Many species are able to alter the environment to their own benefit. Work by Laland, Odling-Smee and others (Laland, Odling-Smee et al. 1996; Laland, Odling-Smee et al. 2001; Griffiths and Gray 2004; Sterelny 2005) has emphasised the importance of niche construction in evolutionary processes. That is, members of many species not only depend on specific environmental factors for their development but also, by their behaviour, shape their environment in ways that affect the chances that they and their descendants will survive and reproduce:

Niche construction occurs when an organism modifies the functional relationship between itself and its environment by actively changing one or more of the factors in its environment, either by

physically perturbing these factors at its current address or by relocating to a different address, thereby exposing itself to different factors. (Laland, Odling-Smee et al. 2001, p.118)

In some cases, the causal impact of niche construction is restricted to the individual organism that constructs the niche. The only spider whose environment is modified by a particular spiderweb is the spider that constructs the web. The same restriction applies to insect cocoons and caddis fly larva houses. In other cases niche construction modifies the extra-organismal environment of later generations. Examples include some birds' nests, termite mounds, female insects' oviposition choices (which afford a ready source of food to her offspring), and soil transformed by earthworms.

There does not seem to be much doubt that niche construction plays a significant role in a wide range of evolutionary processes.

- o The eusocial insects — wasps, bees, ants and termites — make nests that are an important factor in selection for nest maintenance and defence behaviours (Laland, Odling-Smee et al. 2001, p.120). The same applies to the often elaborate burrow systems constructed by badgers, gophers, hedgehogs, marmots, rabbits and other species.
- o Termites do not usually live in termite mounds (though other animals *have* colonised them). One important function of the mound is to regulate air pressure in the nest, which is located under the mound (Turner 2004, p.335). Low pressure in the nest indicates that ventilation is not keeping up with respiration and the termites deal with this by building the mound higher so that it catches more wind and delivers more ventilation.
- o The dams and lodges constructed by beavers are a particularly good example. The construction of these environmental features shapes selection pressures, at the very least in relation to teeth, social system, tail and feeding behaviour.
- o Nest construction is pervasive across major taxa. Of the 9000 bird species nearly all construct nests. There are 9500 species of ants and 2000 species of termites; all live in colonies and almost all build some kind of nest.

There is also some theoretical support for the idea that feedback loops involving constructed niches are capable of playing a major role in population genetics. Work by Robertson (1991) shows that iterated processes that model the creation of evolutionary niches in biological systems can generate important changes in phenotype distribution.

A relatively simple model of niche construction (Odling-Smee 1995) illustrates the dynamics by which constructed niches can modify the selective pressures on the molecular genes that give rise to the construction of the niches.

The model deals with a population of diploid organisms with two genes (at different loci), E and A. Each locus has two alternative alleles, E and e, and A and a. The population's capacity for niche construction is influenced by the frequency of E and e alleles. The amount of some resource, R, in the environment depends on niche construction by past and present organisms. The amount of R in the environment subsequently determines the pattern and strength of selection which feeds back to the population to act on the A locus. The model effectively takes the population as being subject to two distinct kinds of selection. The first is conventional fixed fitness selection, which is assumed to continue to act on the population irrespective of its activities. The second is frequency-dependent selection due to prior niche construction. Changes in the amount of niche construction can send the population down quite different paths, for example, fixing allele a rather than A. In other cases, stable equilibria arise where both a and A organisms persist in the population. The model also shows that there can be lags between the spread of the construction of a particular niche and the evolutionary response to the selective pressure the niche generates.

But while constructed niches, either built anew by each generation or passed on from one generation to the next, may be necessary for the survival and reproduction of many species it is not so clear that the niches themselves are replicated by a selective process.

If a population of termites is placed in a moundless environment that affords them the raw materials for building a mound, they will build a mound. It seems entirely likely that the DNA inheritance of the termites is what determines the kind of mound they build and that at some time in the past variation in niche construction *controlled by the genome* was subject to selection which brought it about that the more fitness-enhancing mounds continued to be built and less fitness-enhancing mounds were selected out (Dawkins 1982, p.200).

The same sort of phenomenon is observed in many other species. Most spiders of a given species build webs according to the same pattern but individual spiders sometimes build webs according to a slightly different pattern — missing a particular concentric ring, for example. The most plausible explanation is that some mutation in the spider's DNA causes it to build aberrant webs: what causes the aberrant web seems to be inside the spider — it does not seem to be a matter of the external environment — and the prime suspect is clearly the spider's DNA. In general, it seems overwhelmingly likely that niche construction in general is a function of the genomic inheritance mechanism. A beaver has an instinct for dam building; beavers do not need an

existing dam to build a dam. And there is really no plausible candidate other than the genome for the source of the dam-building instinct.

If these constructed niches are under the control of the DNA inheritance mechanism, then they are clearly not independently replicated developmental resources; it makes more sense to regard them, with Dawkins, as part of the organism's extended phenotype.³⁹ If we take such a view, we may well ascribe functions to these features. It seems entirely natural — and congruent with the treatment of within-organism phenotypic features — to say that the function of the spider's web is to catch flies, but this does not oblige us to think that the selection that confers these functions operates on a non-genomic inheritance mechanism.

In some cases, as in some mounds, nests and warren systems, collective effects are generated by the activities of one generation and then passed down as a developmental resource to the next generation by which they are further modified. In this case the mound does change over time, but it is still not clear in these cases that good features are selected for and bad features discarded through natural selection.

Even if they were, though, it is hard to find a producer-token-consumer functional structure of the kind that a teleosemantic model of representation demands. We have found such a structure in some genomic cases: roughly speaking, molecular genes have been selected for their capacity to send messages to the ribosome so that particular proteins will be synthesised in response to environmental conditions. In the case of environmental niches, we know (or at least strongly suspect) that they have functions but not that they have the right kind of communicative functions. Suppose tall, narrow termite mounds work better in a particular environment than short, squat ones because they keep the internal temperature more constant and suppose that that is why tall mound colonies have been selected over short mound colonies. We can say that the function of the tall mound phenotype is to keep the internal temperature constant, but this is not a communicative function.

³⁹ A termite mound or a beaver dam is not the work of a single termite or a single beaver so while we can easily regard a spider's web as part of the extended phenotype of that particular spider we cannot regard a termite mound as part of the extended phenotype of any particular termite. Selective pressures acting through termite mounds on the populations that inhabit them are acting collectively, so that the whole colony tends to share the same evolutionary fate so far as the causal influence of its mound is concerned.

Our conclusions here are necessarily tentative but it appears that:

- o some environmental features constructed by organisms are subject to selection. That is, constructed environmental features that help the constructing organisms survive and reproduce are selected for in the sense that organisms which put time and effort into constructing them are more likely to survive and produce offspring that also build or maintain that kind of environmental feature; and
- o some constructed environmental features do have biological functions; but
- o environment features, even ones that are passed directly down from parent to offspring, like beaver dams or termite mounds, do not constitute an independent inheritance system, but are better seen as part of the organism's extended phenotype; and
- o it is unlikely that they participate in the kind of functional structure that our teleosemantic account of representation requires.

7.6 Hormonally mediated inheritance

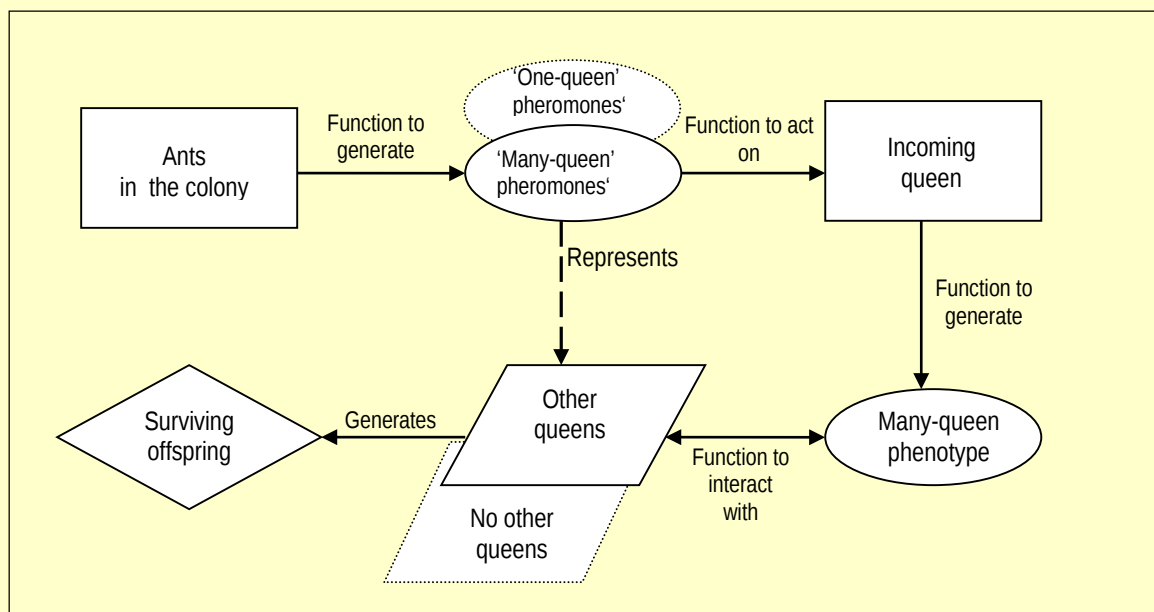
The position of a rodent foetus in the uterus, relative to members of the same or opposite sex, affects both morphology and behaviour in the adult organism. Female Mongolian gerbils that gestate between male foetuses tend to display a more masculine ('androgenised') phenotype and to produce litters containing a significantly greater proportion of sons than the litters of mothers that gestated between female foetuses. Daughters in these mostly male litters are therefore likely to gestate between males and so to display the androgenised phenotype and produce mostly male litters. Consequently, female gerbils tend to inherit the (androgenised or non-androgenised) phenotype of their mothers despite the fact that there are no systematic DNA differences between androgenised and non-androgenised females (Clark, Karpiuk et al. 1993).

Females of the fire ant *Solenopsis invicta* become either large queens, which live in one-queen colonies, or small queens, which live in many-queen colonies. The two types have close to identical DNA. If a female fertilised egg from a many-queen colony is transferred to a one-queen colony, it will develop into a large queen and found a one-queen colony, and vice versa. It appears that the pheromonal environment of the nest is what causes the female egg to develop one way or the other (Keller and Ross 1993, p.121). Effectively, a mutation in a non-genomic developmental resource — the colony that is passed on from generation to generation — has resulted in the divergence of the two types of queen (Griffiths and Gray 1997).

There are two salient questions. Is this kind of inheritance a mechanism capable of supporting natural selection and biological functions? And second, could these functions fit into the consumer-token-producer structure that our teleosemantic account requires?

In relation to the first question, it seems at least possible that this kind of mechanism could support natural selection and that, as a result, the favoured phenotypes could have biological functions. Admittedly in the gerbil case it is rather hard to see what the function of the androgenised phenotype could be, and we should be cautious about adaptationist speculation. In the ant case, however, it seems quite possible that the versatility of the ant colonies provides them with a fitness advantage and the function of the queens' developmental plasticity is to allow them to contribute to the overall fertility of the colony, whether one-queen or many-queen. We should also note that, as an empirical matter, it is not certain whether the different phenotypes in these examples have been subject to selective pressures sufficiently strong and sustained to confer biological functions on them. Still, it may be that the pheromonal mechanism works together with the genomic inheritance mechanism to represent conditions in the colony at which a new queen is arriving. The production of appropriate hormones by the ants in the colony signals to the incoming queen signals the status of the colony as one-queen or many-queen, and prompts a suitable phenotypic response on her part. The functional structure is set out in Figure 13.

Figure 13: Pheromonal inheritance in fire ants



It is important, though, to note the limitations on representation of this kind.

First, there are few examples. That does not mean that this inheritance mechanism — at least in collaboration with the genomic system — cannot underwrite biological function and hence, potentially, representational content; but it does mean that there seems to be relatively little representational content generated through this mechanism.

Second, these seem to be very limited inheritance mechanisms. In these examples, at least, only females are involved and in each of the examples given above, there are only two phenotypes available: androgenised or non-androgenised phenotypes in the gerbil case and large queen or small queen in the fire ant case.

Third, all the hormones that do the mediation are built in accordance with DNA sequences. So the mechanism depends on DNA sequences to work. That alone does not mean it is incapable of underwriting biological functions: molecular genes themselves need a complex array of cellular developmental resources to perform their functions. It does, however, establish an asymmetry between the nucleic acid inheritance mechanism and the hormonal mechanism: natural selection and evolving lineages can arise without the hormonal inheritance mechanism but not without the genomic inheritance mechanism.

7.7 Membranes

Membranes consist of a fluid layer of lipid molecules with a large variety of proteins embedded in it. Membranes grow by insertion of new lipid and protein molecules into existing membranes. They then divide into two daughter membranes which may be very similar in composition — as, for example, in cell division or organelle division in eukaryotes — or very different — as in vesicle budding or endocytosis (Cavalier-Smith 2004).

The most obvious functions of some membranes, like the endoplasmic reticulum, is to hold the cell together. Others form the intracellular boundaries of organelles in eukaryotic cells.

Membranes also seem to play an important role in the expression of molecular genes. For example, protein synthesis begins in the cytosol when an mRNA molecule passes out of the nucleus through a nuclear pore and triggers the assembly of a translational complex at the ribosome. Proteins that move through the membrane system have a signal sequence at the N-terminal end of the protein. The signal sequence suspends synthesis, which cannot be resumed unless the sequence joins up with ‘docking proteins’ embedded in the endoplasmic reticulum. These are coded for in DNA but there must always be receptors embedded in the endoplasmic reticulum in order for any synthesis to occur. (Moss 2003, p.82).

There is fairly strong evidence that at least some membranes are self-replicating in the sense that an existing membrane is necessary for the synthesis of a new one.

- o A number of different types of membrane — for example, the rough endoplasmic reticulum, plasma membrane and the outer membrane of plastids and mitochondria — grow only from pre-existing membranes of the same kind. Cavalier-Smith calls them (perhaps a little tendentiously) ‘genetic membranes’. If one type of membrane were lost from an organism’s cells but all the molecular genes encoding its proteins and all the lipid-synthesising machinery remained, the membrane could not be reconstituted because the proteins would not have access to a template membrane in which they could be embedded.
- o In general, membrane polarity and topology (and possibly membrane protein and lipid composition) are key features transmitted (at least in part) by an inheritance mechanism that relies on one membrane acting as template for the making of another.
- o Moreover, the distribution of receptors in the membranous compartments of the cell is preserved through cell division throughout the entire cell lineage to create what Moss (2003, p.85) calls ‘the self-templating, highly differentiated, decay-resisting, far-from-equilibrium nature of the membrane system’.

So it appears that there is replication going on here that is not dependent only on DNA but also on the presence of membranes to act as templates for the production of new ones. And, unlike the hormonal mechanisms we looked at in the previous section, membranes are fundamental features of all cells: the structural integrity of all cells depends on membranes that reproduce using the template mechanism (in conjunction with the genome, of course). So a gene-centric teleosemanticist cannot wave away membrane reproduction as a biological oddity of limited importance.

Still, while we may agree with Moss and Cavalier-Smith about a distinctive role for membranes as templates for their own reproduction, we need not believe that this mechanism underpins selection and biological function, let alone that it underpins functions that have the producer-token-consumer structure that our teleosemantic model requires.

First, membrane inheritance is a limited, sample-based form of replication (Sterelny 2005). A sample of a particular type of membrane is needed to act as a template for replication to occur. The kind of compositional structure displayed by DNA and associated nucleic acids is absent from the membrane inheritance mechanism. For this reason, the range of variation generated by the

inheritance mechanism is likely to be limited, and indeed it appears that only 18 different types of membranes have evolved over the entire history of life on earth.

Second, membrane templating does not seem to have given rise to *representational* functions. Like everything else, membranes are affected by the (intracellular) environment but they do not appear to generate tokens in response to their cellular environment that communicate with other systems to allow them to deal successfully with that environment, or to track features of that environment in ways that conduce to their survival and reproduction.

At this point we can conclude that self-templating between generations of membranes does not give rise to representational functions.

7.8 Inheritance of acquired characteristics

It used to be a central tenet of genetics that phenotypic characteristics acquired by an organism could not be passed down to the next generation. That is, nucleic acid structures in the germ cells were thought to be the only mechanism by which traits could be passed from generation to generation. More recently, though, a number of examples have emerged which suggest that in some cases characteristics can be transmitted across generations, even though germ line DNA has not been altered. The mechanisms involved are not well understood, so we need to be cautious, but it is beginning to look as though there may be other ways that phenotypic characteristics can be passed down from generation to generation.

- (1) Trypanosomes are parasitic, unicellular eukaryotes that cause sleeping sickness in humans and are carried by the tsetse fly. Each organism has a single whip-like structure ('flagellum') that winds around the cell in a spiral path from front to back. During the cell division that gives rise to a daughter cell, a connection arises between the parent's flagellum and the daughter's flagellum which determines whether the daughter's flagellum is located at the head or tail end of its body (Moreira-Leite, Sherwin et al. 2001, p.610; Pal and Hurst 2004, p.356).
- (2) Diploid yeast cells polarise and reproduce by budding from their poles. Rax2, a membrane protein, acts as a mark for polarisation and budding. Rings of Rax2 are inherited at the cell cortex and remain unaltered on cell surfaces for many generations of cells, although the DNA of the marked cells does not differ from that of unmarked cells (Chen, Hiroko et al. 2000, p.1975).

- (3) It is possible, though it has not been definitively established, that the initial polarity of animal eggs is influenced by the asymmetry of surrounding follicle cells. A number of asymmetrically distributed proteins, particularly leptin, are found both in the cortex of the mammalian egg cell and in the surrounding follicle cells, suggesting that the follicle may play a role in the establishment of asymmetries in the egg cell and hence in the early embryo (Godfrey-Smith 1994; Gardner 2001, p.273)
- (4) Flax plants that are treated with a range of chemical fertilisers display a distinctive phenotype with more branches and broader leaves than wild type plants. These traits are passed on to successive generations via the seeds but not by alteration of the base sequence of the organism's DNA. Instead, the cells of treated plants respond to the fertiliser by amplifying particular regions of the genome (Maynard Smith and Szathmary 1995, p.247).⁴⁰
- (5) Somatic recombination is a process in the early stages of the development of the immune system. It combines a range of gene segments, nearly at random, so as to procure the synthesis of a large number of different antigens. In a number of plant species, increased rates of somatic recombination appear in response to various stresses, including increased ultraviolet radiation and a variety of pathogens (Bond and Finnegan 2007). In some cases, these rates persist in later, unstressed generations, though no DNA changes distinguish stressed and unstressed plants (Molinier, Ries et al. 2006). We do not know what mechanism underlies the transmission between generations, although Bond and Finnegan speculate that RNA-directed changes in chromatin structure (see section 7.3 above) may be responsible. Molinier's work establishes that the increased recombination persists for at least four generations.

In all these cases it appears that phenotypic characters are passed from generation to generation by mechanisms other than the genome.

⁴⁰ Amplification occurs when a molecular gene or DNA sequence is multiplied to produce numerous copies within the chromosomes (Lawrence 2005, 32). Amplification can now be induced in the laboratory. The classical case of naturally occurring amplification is the successive duplication of haploid chromosomes in particular tissues of *Drosophila melanogaster* (Hartwell et al 2000, 410).

However, in the first four cases — the paramecium's cortex, the trypanosome's flagellum, the rings on the yeast cells and the polarity of animal ova — it is not clear that the traits passed on bring fitness differences with them. It is at least doubtful that these inherited characters are selected for and, as a result, doubtful that they have biological functions.

In the fifth case, amplification in flax plants, it seems doubtful that the function of the distinctive broad-leafed phenotype enters into the functional structure necessary for representation on the teleosemantic views of representation that we have been considering. It is not clear how the new phenotype could help the plant deal with a fertiliser-rich environment but even if it were fitness-enhancing and selected for its fitness enhancing effects, it's not clear that its function is a representational function. Unless we find out something more, it appears to be no more than a normal biological function, not a representational function.

The last case, increased somatic recombination in response to environmental stressors, again seems to involve the intergenerational transfer of phenotypic traits by non-genomic means. While the range of variation generated by environmental stressors is less certain, impacts on fitness seem overwhelmingly likely, given the key role of antibodies in resisting damage to the organism. Moreover, since the increased recombination arises in response to an environmental change and assists the organism in dealing with that change — that is, it confers differential fitness on affected plants — it seems to meet the same criteria for pushmi-pullyu representation as we identified in the galactosidase case (section 3.2).

Like chromatin marking, this is not an inheritance mechanism independent of the genomic inheritance mechanism. There is definitely some non-genomic inheritance going on here but the phenotypic variation it produces is generated in cooperation with, and could not arise without, the genomic inheritance mechanism.

So this appears to be a function-conferring inheritance mechanism when working in combination with the genome and, since the function of the amplification appears to be to track changes in the environment, I think this is a case where a non-genomic inheritance mechanism working with the genome *is* underpinning pushmi-pullyu representation.

7.9 Prions

Prions are particular types of protein molecules, produced by the cells of a host organism and composed of around 210 amino acid residues. Their covalence structure is identical with that of a normal, non-pathological protein produced within the organism but they differ in their three-

dimensional configuration.⁴¹ Prions are infectious agents: a prion is able to make contact with another protein molecule and act as a template for its conversion into another prion.⁴² These are self-templating particles but, unlike DNA there is no specialised replication machinery. ‘The ability of a structure to be reconstructed in daughter cells is inherent in its organisation’ (Jablonka and Lamb 2005, p.126).

In the fungus *Podospora anseria* and the yeast *Saccharomyces cerevisiae* four different strains of prions can be transferred from one cell generation to the next. Yeast and fungal prions seem to do their hosts no harm and may possibly be beneficial (Tuite 2004, p.265) but mammal prions are pathogens to their hosts, causing bovine spongiform encephalopathy (mad cow disease) in cattle, scrapie in sheep, and *kuru* and Creutzfeldt-Jakob disease in humans.

There are strains of prions where a single protein can fold into structurally distinct infectious states that cause distinct heritable phenotypes but without any change to the underlying amino acid sequence of the protein or to the genetic constitution of the host (Tanaka, Chien et al. 2004, p.323; Toyama, Kelly et al. 2007, p.233).

Jablonka and Lamb (2005, p.153) are right when they say that almost any amount of variation will involve differential fitness of at least some degree so, since different phenotypes accompany different folding structures, selection between different folding structures of the one protein must surely be possible.

Moreover, there doesn’t seem to be anything to prevent the occurrence of a new prion, with the same sequence of amino acids as an existing form, but with a different folding structure. As with other organisms, such a novel phenotype may be fitter or less fit than other phenotypes.

⁴¹ Two molecules have identical covalence structures if (a) they are composed of the same number of atoms of each element (e.g. two carbon and four hydrogen) and (b) the covalent bonds between the atoms in the molecules are identical. A covalent bond is the most basic, and strongest, bond between two atoms, arising when the two share one or more electrons.

⁴² The idea that a purely protein structure, without nucleic acid, could be responsible for *kuru*, bovine spongiform encephalitis and other diseases was canvassed for the first time only in the 1980s. While some researchers still suspect that nucleic acids play a part in prion transmission, it seems increasingly likely that yeast prions, at least, are purely protein particles.

Still, there are four reasons to doubt that protein folding constitutes an independent inheritance mechanism.

First, prions do not seem to generate much variation. Remember a prion is just a steric modification of a protein — that is, the same protein (in terms of amino acids, their constituent atoms and their covalent bonds) with a different three dimensional configuration. As a matter of molecular biology, there are simply not all that many such configurations available for any given protein.

Second, the range of prions that we know about at this point is relatively limited, certainly not sufficient to back up a claim that a prion itself or some phenotypic feature (either of the prion or of the larger organism within which it is located) is the product of a selective process grounded in variation between generations of prions.

Third, and perhaps most importantly, the folding pattern of a protein has its phenotypic effects only by virtue of the primary structure of the protein: different primary structures yield different phenotypic effects, regardless of the folding pattern. There *is* some evidence to suggest that the [PSI⁺] prion in *S. cerevisiae* (brewer's yeast), may increase the evolvability of yeast by causing read-through translation and thus revealing hidden variation in untranslated regions of DNA (True and Lindquist 2000, p.477; Masel and Bergman 2003, p.1498).⁴³ But it is clear that even if prions can boost evolvability it is still evolvability underpinned by the genomic inheritance mechanism, not by prion to prion inheritance.

For this reason, I think we should see the kind of protein folding that produces prions as a very limited adjunct to the genomic inheritance mechanism rather than a mechanism on its own account.

7.10 The story so far

In summary, then these seem like a set of interesting, but perhaps marginal cases where our understanding of the biology involved is quite imperfect. It is certainly not impossible that some of these non-DNA inheritance mechanisms could underpin selection, biological functions and, in particular, biological functions that participate in a representational structure.

⁴³ Read-through translation (or transcription) occurs when translation continues past a termination codon in an mRNA transcript.

So what does the overall picture look like? Table 2 summarises the conclusions regarding the eight types of non-genomic inheritance mechanism we have examined in this section.

Table 2: Developmental resources, natural selection and representational functions

Mechanism	Example	Replication	Variation	Differential fitness	Supports function?	Representational function?
Chromatin marking	Methylation patterns	Yes	Yes, with the genome	Yes, with the genome	Yes, with the genome	Maybe, with the genome
Symbionts	Luminescent bacteria in squid	Yes	Limited, and with the genome	Yes	Yes, with the genome	Maybe, with the genome
Niche construction	Termite mound	Not independent of the genome	Yes	Yes	Not independent of the genome	No
Hormonal environment	Mongolian gerbil	Yes	Very limited	Yes	Limited at best	Doubtful
Membranes	Endoplasmic reticulum	Yes	Limited	Possibly	Possibly	No
Increased amplification	UV light in <i>Arabidopsis</i>	Yes	Yes, with the genome	Yes, with the genome	Yes, with the genome	Yes, with the genome
Other non-genomic mechanisms	Polarity of bacterial flagella	Yes	No	Possibly	No	No
Prions	[<i>PSI</i> ⁺] in yeast	Yes	Yes	Possibly	Doubtful	No

Still, we do not want to be too narrow here. Some of these developmental resources seem to possess biological functions, conferred by their selectional history. So representation among developmental resources is not rife but it is more widely distributed than the genome itself, although the genome remains the predominant source of representation.

We also need to acknowledge that in many cases our knowledge of the mechanics and, particularly, history of these non-genomic inheritance mechanisms is very limited, so that the conclusions summarised in Table 2, so far as they rely on empirical fact, must be regarded as tentative.

7.11 Cooperating inheritance mechanisms

We have seen examples where various non-genomic inheritance mechanisms — symbionts, prions, chromatin marking, chromosomal amplification in response to stress — exert an

influence on gene expression and produce heritable phenotypic variation without genomic mutation. In all cases, though, the non-genomic inheritance mechanisms depend on the genome to exert their influence on phenotype. So the picture is not a simple one. In order to get a phenotype we need more than just a genotype and some unstructured, extra-organismal developmental resources. Other inheritance mechanisms impact on the workings of the genome but do not affect the phenotype with anything like the same specificity or range as the genotype does.

Here on earth, the genome is the major engine of heritable phenotypic variation. Other inheritance mechanisms, if they underpin selection at all, do so by interacting causally with the genomic inheritance mechanism. Possible worlds in which the genome remains constant and the only source of heritable phenotypic variation is the actual world's non-genomic inheritance mechanisms are pretty remote from this one. The necessary conditions for the emergence and maintenance of evolving life forms, given the laws of nature (whatever they are), are so imperfectly understood, that I do not think anyone could be confident of the answer at this point.

If we identified some combination of inheritance mechanisms that:

- o was able to generate enough phenotypic variation to underpin a selective process;
- o did so in the absence of genomic variation;
- o did not rely on affecting the expression of molecular genes to do so; and so
- o underpinned not just any biological function but a representational biological function;

we would indeed have the interesting situation where representational content was generated through two quite distinct evolutionary mechanisms. This is neither conceptually nor nomologically impossible. In our present state of knowledge though, it seems that even in collaboration, non-genomic inheritance mechanisms need to work through the genome to generate phenotypic variation.

7.12 Conclusions

In summary, then, we may conclude that:

- o some non-genomic inheritance mechanisms are capable of underpinning a selective process without accompanying variation in the genome;

- o some of these processes give rise to phenotypic variations that probably possess biological function, though we cannot be entirely sure at this point;
- o these functions, however, are probably not representational functions, though again, we cannot be entirely sure;
- o the fact that no non-genomic inheritance mechanisms underpin representational functions without accompanying variation in the genome is a contingent matter;
- o some non-genomic inheritance mechanisms interact with genomic variation to underpin biological functions; and
- o some of these biological functions appear to be representational functions (though only of the most basic kind); but
- o representation arising from these functions always relies — to some extent — on the genome.

Where are we up to, then? So far I have argued that a teleosemantic view of representation, based on an aetiological view of biological function, is both a flexible and plausible account of these concepts. When we apply them to the genome we can identify representation in the relationship between molecular gene and synthesised protein, and between molecular gene and environmental conditions. It is harder, however, to identify representation in the relationship between molecular gene and phenotype: the key problem is the absence of a single, function-bearing consumer device that responds to a representational token by generating a particular phenotype. We have also discussed the characteristics of the genome that make it such a versatile representational system — its compositionality and the arbitrariness of the codon-amino acid assignments that constitute the ‘genetic code’. In the last section, we asked whether inheritance mechanisms other than the genome can confer biological functions and whether any such mechanisms confer functions that conform to the producer-token-consumer structure that is characteristic of representation on a teleosemantic view. I have argued that we should answer the first question in the positive but should be more skeptical in relation to the second: there is clearly no logical or biological reason why a non-genomic inheritance mechanism could not confer functions; but as a matter of fact it seems that such mechanisms are relatively rare and that where they do operate, they do not, unambiguously, generate representational functional structures.

In the next sections, we will discuss two fundamental criticisms of the project I have been pursuing. First, it is possible to argue that identifying representation in the genome is

epistemologically second-rate — that representational talk about genomic phenomena is merely metaphorical or analogical or that representational systems provide no more than a useful model for some genomic phenomena. Second, it is possible to argue that, even if we can legitimately identify representation in the genome, doing so serves no purpose — that representational talk about genomic phenomena adds nothing to our understanding beyond what is made available by the functional talk that underpins representation on a teleosemantic view. Let's consider the first family of arguments.

8 Metaphor, analogy and models

In this essay I have been arguing that, on a teleosemantic view of representation, some nucleic acid structures, particularly mRNAs, represent a variety of features of the world — proteins, features of the intracellular environment and features of the extra-organismal environment.

That is I am arguing that, on a teleosemantic view of representation, nucleic acid structures — in some cases at least — *literally* represent these things. I am taking teleosemantics as a particular naturalistic, theoretical reduction of the representation relation and attempting to show that on this account, nucleic acid structures (like natural languages and animal signaling systems) possess representational content. In other words, I am arguing that:

- o X represents Y iff X and Y are in some (pretty complicated) relation *R* which is cashed out in terms of naturalistic concepts like cause, frequency, possibility, law of nature, as well as the concepts belonging to the special sciences; and
- o some nucleic acid structures bear the relation *R* to particular proteins, features of the intracellular environment and features of the extra-organismal environment. (I am also arguing that these propositions matter, but that is the subject of the next section.)

In arguing for this view I have identified and described correspondences between the functional structures in which some nucleic acid structures participate and functional structures in which the elements of paradigmatic representational systems participate. Under a teleosemantic view, such structures are taken to be constitutive of the representation relation. Such structures arise because there is also a correspondence between the macro environment in which inter-organismal representational systems operate and the micro environment of the cell. Both environments pose coordination challenges that can be addressed by representational systems.

Still, it is possible to argue that even though there are genuine correspondences between functional structures that involve nucleic acid structures and the functional structures that characterise natural languages, the relationship between the two systems is not sufficiently close to warrant attributing representational content to nucleic acid structures.

This is not implausible. The use of representational language to describe genomic phenomena is endemic in molecular biology and in some cases — e.g. ‘the blueprint for an organism’, ‘reading the book of life’ and ‘reading the story in DNA’ — it seems clear that the use of representational language relies not on the fact that natural language and genetic phenomena are both

representational systems but on some looser relationship between the two. More particularly, we may think that:

- o statements that use linguistic terminology to describe genomic phenomena are *metaphors* and are not literally true; or
- o while there are *analogies* between some genomic phenomena and paradigmatic representational systems, they fall short of the standard of strength needed to justify calling the genomic phenomena representational; or
- o while paradigmatic representational systems may serve as a useful *model* for understanding some genomic phenomena — or vice versa — we are not justified in making the stronger claim that the genomic phenomena literally possess representational content.

In this section I will consider, and argue against, each of these positions.

8.1 Metaphor

Griffiths (2001) and others (Kitcher 2001; Levy 2011) have argued that talk of biological information is merely a metaphor — not part of biological theory proper.

Despite the appearance of the notion in the title of his article — ‘Genetic Information: a Metaphor in Search of a Theory’ — Griffiths does not actually spend much time talking about metaphor. He (2001, p.395) quotes Sarkar as saying, ‘there is no clear, technical notion of “information” in molecular biology. It is little more than a metaphor that masquerades as a theoretical concept.’ And he says (p.408):

this series of points [made by Maynard Smith] is clearly meant to suggest that since the genetic code is “real science” and not mere metaphor, it is only a matter of time before other information talk in biology becomes real science too.

Still it is clear enough that Griffiths (and the others) think that linguistic (or ‘scriptural’) concepts are not a part of our best theory of genomic phenomena. Perhaps they do no more than add colour or advance a vague, and non-truth valued, set of suggestions about the characteristics of the genome. So I think the reading of metaphor he has in mind is a pretty traditional one under which:

- o the content of metaphorical statements depends in one way or another on the content of other, non-metaphorical statements; and
- o metaphors are indirect — albeit sometimes powerful — ways of saying what we can also say, more clearly, using non-metaphorical language.

But this general notion of metaphor is really far from clear. Where and how do we draw the line between literal and metaphoric language? Can metaphorical statements be true or false? Can they enter into inferential relationships with other statements? Can they be paraphrased into literal language without loss of meaning? There is no consensus on these questions in the linguistic or the philosophical literature. Some people think that metaphor is illogical, second rate and misleading (Turbayne 1962); some think it is inherent in, and essential to, our most basic conceptual frameworks (Lakoff and Johnson 1980).

We can hardly evaluate the claim that use of linguistic terms to describe genomic phenomena is *merely* metaphorical without being clearer about what we mean by metaphor, and about what the consequences are if we decide that some particular statements — here, of course, statements about genomic processes that use linguistic terms — are metaphorical.

We will consider this claim in light of two different accounts of metaphor, and assess the consequences for the theses I have been defending in this essay. I will argue that on the first two views, which draw an intuitively appealing distinction between literal and metaphorical language, the claim that talk about nucleic acid structures bearing representational content is merely metaphorical rests on the adequacy or otherwise of the theory of content that underpins attribution of content to those structures. In other words, if we have a good theory of content and that theory warrants the attribution of representational content to nucleic acid structures, then we may take such attributions to be literally true. That of course, is my position.

First, let us take a Gricean perspective on language. In literal utterances, what is said is taken to be the proposition expressed by an utterance and this proposition is taken to be the product of the contents of the words uttered and the rules for their semantic composition.⁴⁴ The literal content of a semantic token is whatever is constant in content across all uses of the type to which the token belongs. It is only if the context of the utterance makes the normal, or literal, content

⁴⁴ The same compositional approach applies under a Millikan-style teleosemantic account, under which the functions of the lexical and syntactic features of a sentence are coordinated to yield a more complex, semantic function (for example, Millikan 1984, 190).

inappropriate that a metaphorical content is implicated. Metaphorical content involves ‘that part of what is communicated that is determined, not by the rules of language, but by more general (inferential) constraints, such as the Gricean conversational maxims that demand clarity or relevance in a speaker’s contribution’ (Wearing 2006, p.311).

So if Meleager and Neophron are watching Charmides the wrestler struggling with an opponent and Meleager says to Neophron, ‘He is a bulldog’, context establishes that he cannot be literally claiming that Charmides is a bulldog, which is the meaning determined by the rules of language: he is clearly not. Since a literal interpretation is not tenable, the next way to make sense of the remark is to try and find an *X* where *X* is a well-known characteristic of bulldogs possessed by Charmides: determination or unwillingness to relinquish a physical hold on an adversary, or something of the kind.

Generally, what is said by an utterance is determined by the rules of language unless the context of the utterance, its pragmatics, make this untenable. In that case, we appeal to a set of interpretive conventions to try to make sense of the utterance.

On this view, I have a straightforward response to the claim that talk of nucleic acid structures bearing representational content is merely metaphorical. The teleosemantic theory presented in section 3 and the applications of that theory presented in section 4 go to show that the literal interpretation of a range of claims like ‘this mRNA does not bear representational content’ or ‘nucleic acid structure *X* represents cellular state of affairs *Y*’ is quite tenable. There is no need to seek a metaphorical interpretation of such claims because their literal content is perfectly appropriate in usual contexts. So, for example, I argue that, under a teleosemantic account of representation, the literal content of an utterance of ‘nucleic acid structure *X* represents cellular state of affairs *Y*’ is simply its literal meaning determined by the meanings of its elements and the rules of English. In usual contexts, it fulfils the requirements of the normal Gricean rules — truth, relevance, perspicuity and so on — without the need to seek another metaphorical content by reference to these criteria.

Clearly the meaning of ‘representational content’ depends on the teleosemantic theory of content I have adopted in this essay and if you do not like that theory, you may not agree that the utterance is literally meaningful. In this case, dismissing semantic talk about nucleic acid structures as mere metaphor boils down to the claim that there is no good theory of representational content that attributes representational content to nucleic acid structures. The claim that attributing representational content to nucleic acid structures is metaphor adds nothing to the underlying disagreement about the nature of representational content and whether nucleic acid structures bear it.

Second, an historically popular view of metaphor is that it is essentially ornamental, a dramatic way of saying something that could also be said in literal language (Stern 2001, p.189). So in the wrestling example above, Meleager could have said, ‘Once he gets a hold it is very hard for his opponent to make him let go’, and conveyed the same meaning. The bulldog metaphor adds colour but conveys no different content.

If we interpret Griffiths in this way, he could be claiming that teleosemantic talk of representational content in the genome adds nothing to talk of biological functions (and the selective history that underpins them). Levy (2011) takes a middle view on which information talk in biology is ‘serious but isn’t literally true’: such talk is ‘using a schema ... so as to bring to the fore coarse-grained causal properties of the processes in question’. The clear implication is that there is some *other* kind of talk — the real, flat, scientific talk — that also describes the processes in question but is literally true.

Certainly, on a teleosemantic view, statements about representational content borne by nucleic acid structures can be paraphrased as complicated sets of statements about biological function and evolutionary history. This does not, however, entail that talk of representational content in the genome is merely ornamental. When we successfully cash out a high level theory in terms of a lower level theory we can usually, in principle at least, express higher level statements in terms of lower level statements. So, for example, we might cash out consumer price inflation in terms of particular sets of transactions — purchases of (more or less comparable) consumption goods — in a particular area in successive periods. That does not, however, mean that talk of consumer price inflation is merely ornamental.

There are deep differences between the kind of paraphrase that transforms a metaphorical statement into a literal one and the kind that transforms a statement in a higher level theory into a statement (or a set of statements) in a lower level theory.

- o *Context independence.* Reductive paraphrasing is context independent in a way that metaphorical paraphrasing is not. The rules for paraphrasing a statement in the higher level theory into the lower level theory are clear and well-defined. For example, a statement like ‘mRNA *X* represents protein *Y*’ can be paraphrased into lower level language that cashes out representation along teleosemantic lines, appealing in specific, explicit ways to notions of biological function, selection, fitness and so on. By contrast, an ornamental metaphor in everyday language — and this is not to say that all metaphors in everyday language are ornamental — is not paraphrased into literal language by such an explicit set of rules. The basis of the ornamental metaphor differs more from case to case and must be inferred from the context (Bezuidenhout 2001, p.158).

- o *Wide structural preservation.* Reductive paraphrasing preserves the logical structure of the higher level theory in the lower level theory. So a metaphor like ‘he is my sword and my shield’, if it means anything, means something like ‘he both attacks my enemies and protects me from their attacks’, but that is as far as it goes. Talk of greaves and bosses and hafts and so on, has no counterpart in the literal language. Indeed, attempts to extend such metaphors further and further into their logical neighbourhood often become ridiculous.

Mere paraphrasability, then, is not enough to distinguish metaphorical statements from ‘proper’ theoretical statements. Clearly, the fact that a statement in the higher level theory can be paraphrased as a set of statements in the lower level theory does not establish, or even suggest, that the statement in the higher level theory is ornamental in some way, or is not literally true. We can reduce talk of the temperature of a gas to talk of the kinetic energy of the atoms of which it is composed but that does not entail, or suggest, that temperature talk is just ornamental or vague or not literally true. Much the opposite: the whole point of theoretical reduction is to strengthen the higher level theory by giving it solid underpinnings in the lower level theory and to strengthen the lower level theory by extending its reach and coherence with other theories.

So there is a fundamental difference between paraphrasing ornamental metaphor into literal language and paraphrasing statements in a higher level theory into statements in a lower level theory.

In summary, under the characterizations of metaphor considered above, whether or not it is reasonable to regard representational talk in molecular biology and genetics as merely metaphorical boils down to whether we think that:

- o a teleosemantic account of representation is a good one;
- o that account applies to genomic phenomena; and
- o applying that account to genomic phenomena is theoretically fruitful.

These are open questions, of course, which I deal with elsewhere in this essay, but together they seem to cover the substance of the claim that representational talk in relation to genomic phenomena is merely metaphorical.

8.2 Analogy

Another way of characterising the relationship between paradigmatic representational systems and nucleic acid structures which admits some commonality between the two, but falls short of the kind of theoretical unification that I am advocating in this essay, is as an analogical relationship.

What do we mean by an analogy? Consider the relationship between sound and light, illustrated in Table 3 (Hesse 1963, p.66).

Table 3: Analogy between sound and light

	Properties of sound	Properties of light
causal relations	Echoes	Reflection
	Loudness	Brightness
	Pitch	Colour
	Detected by ear	Detected by eye
	similarity relations	

In this kind of table, the causal relations that link the items in the first column follow much the same pattern as the causal relations that link the items in the second. As a consequence, a similarity relationship holds between the two items on each row of the table.

Some analogies are closer than others. In a close analogy:

- o a good number of properties on both sides of analogy are linked together, i.e. the table has a good number of rows — the more the better;
- o the linked properties are measurable — so that we can tell whether the causal relationships between the items on either side of the analogy correspond more or less closely; and
- o the properties are linked together in a calculable way — not only are the individual properties measurable, but the links between them are as well.

These three characteristics — the number of properties linked in a causal network, the measurability of the properties identified, and the precision with which that network can be specified — can together be thought of as constituting the strength of the relationships between the elements of a particular column. When the same pattern of relationships is shared by the other column we have a close analogy.

In the case of sound and light the analogy is fairly close. So, for example, measures of loudness and pitch are connected by the same mathematical relationship as connects measures of brightness and colour. This is a strong and fruitful relationship.

As an example of a weaker analogy we can look at the relationship between a (patriarchal, agrarian) family and kingdom (see Table 4).

Table 4: Analogy between family and kingdom

	Properties of family	Properties of kingdom
causal relations	Up to dozens of members	Up to millions of subjects
	Run by patriarch	Run by king
	Patriarch has right to exile members	King has right to kill subjects
	similarity relations	

Here the analogy is less strong because:

- o the properties identified are few in number;
- o the ‘run by’ property — at least without further specification — is hard to measure;
- o the circumstances in which the right to exile and the right to kill are characteristically exercised are different, so that it is not possible to use the behaviour of a family to predict the behaviour of a country in the same way as it is possible to use the behaviour of sound to predict the behaviour of light;
- o nearby properties in the two domains, family and country, do not map onto one another. So, for example, the relations between family members and subjects of the kingdom are quite different: the family members know one another, the subjects do not; the family members are bound by strong obligations of mutual assistance, the subjects aren’t etc.

For these reasons, the analogy is relatively weak. The causal patterns in one domain do not correspond closely to those in the other.

Analogies are very important in the practice and pedagogy of science. Working scientists use analogies between very different domains to generate theories and hypotheses that can, all being well, be tested by experiment or further observation. Such heuristic use (Nersessian 1988) is quite different from the use of analogical reasoning in the statement of a particular theory, though it is a perfectly legitimate practice and a perfectly legitimate subject for philosophical or psychological investigation.

In a famous example, August Kekulé, a German organic chemist who was investigating the chemical structure of benzene, reported a day dream featuring the ouroboros, a mythical serpent eating its own tail.⁴⁵ This, he claimed, inspired his theory of benzene's structure, based on carbon-carbon bonds. Further experiment confirmed his hypothesis. Of course Kekulé didn't believe there really was an ouroboros and he certainly believed that benzene exists. The usefulness of the analogy here was as a heuristic device. Clearly the two domains do not have to have much in common; in the Kekulé case it was not even necessary that they were both part of the actual world.

The benzene-ouroboros analogy wasn't a very close one. The only real commonality between the two was the ring configuration of snake and molecule. Even where the analogy is much closer, however, there may be no available explanation of why the analogy holds. So, for example, Mathieu's equation is:

$$\frac{d^2y}{dx^2} + [a - 2q \cos(2x)]y = 0.$$

It is used to describe a number of quite disparate physical phenomena: the vibration of elliptical membranes, the equilibrium of an acrobat in a balancing act (Hesse 1963, p.50), as well as the motion of particles in electromagnetic traps and the inverted pendulum (Coisson, Vernizzi et al. 2009). In all these cases the same well-defined formalism applies to corresponding kinds of physical entities, so that by the standards set out earlier, the analogy between the different domains is a close one. There does not, however, seem to be a single explanation of why

⁴⁵ The ouroboros, under different names, appears in a wide range of cultural contexts, including Ancient Egyptian mythology, the dialogues of Plato (*Timaeus*, 33), the Upanishads, and Norse mythology.

Mathieu’s equation applies to all of these phenomena. We know that the different phenomena obey the equation but not why they do.⁴⁶

Another example (Juthe 2005, p.8) might be Hobbes’s analogy between a political state and a human being, where sovereignty is taken as analogous to the soul, magistrates to the joints, wealth to strength, concord to health and so on. Again, even if we think the analogy is a close one, we do not have an explanation of why it is: states come into being through quite different processes from those that give rise to the morphology of the human being; the succession of states in human history has no obvious correspondence with the lineage of human beings. There appears to be no common explanation of the analogy, whether phylogenetic or ontogenetic.

My claim is that the links between genomic phenomena and other representational systems are qualitatively different because they go beyond causal isomorphism between the two sides of an analogy. The reason is that the relationship between nucleic acid structures and the tokens of paradigmatic representational systems is underpinned by the same evolutionary process: they are both the products of devices that have been selected to perform in functional systems that share the same structure. The analogous processes have the same causal explanation, an evolutionary explanation. And this explanation has the same pattern in both cases.

In terms of the tabular presentation used above, there a strong correspondence between the two columns (see Table 5).

Table 5: Analogy between nucleic acid structures and natural language tokens

	Properties of nucleic acid structures	Properties of natural language tokens
causal relations	Function of a kind of mRNA is to allow the cell to adapt its behaviour to particular states of affairs in its environment	Function of particular words and sentences is to allow humans to adapt their behaviour to particular states of affairs in their environment

⁴⁶ I suppose if the whole of physics were deducible from the fundamental constants and the boundary conditions at the big bang — which it might be — then, in a trivial sense, the fact that Mathieu’s equation describes the vibration of elliptical membranes and the fact that it describes the motion of the inverted pendulum share a common explanation: they are both inevitable consequences of the values of the fundamental constants and the initial conditions at the big bang. But that does seem a trivial sense: all physical phenomena share *that* explanation.

	A particular kind of mRNA is produced by systems selected for producing that mRNA	Particular words and syntactic structures are produced by systems whose function it is to produce those words and structures
	Different mRNAs have the function of evoking different responses in the consuming system (ribosome etc)	Different words and sentences have the function of evoking different responses in the hearer.
	Etc	Etc
	similarity relations	

The difference between this case and the Mathieu case or the Hobbes case is that the pattern of relationships in each column is explained by the *same* causal-historical process. Each pattern is the result of selective forces shaping signaling systems that allow consumer organisms, or sub-organismal systems, to navigate their environments successfully. To take another example, consider the analogy between English and Swahili. Not only do we find a close correspondence between the elements in the two columns and between the relationships that link the elements in either column but we find the same causal-historical explanation for the similarity of the patterns: both languages are the product of cognitive systems which have the function of coordinating human behaviour so as to promote the survival and reproduction of the hearer.

So while there clearly is an analogy between some genomic phenomena and paradigmatic representational systems, it is not *just* an analogy, but one underpinned by a common explanation of why both sides of the analogy follow the same causal pattern. That explanation is the selection-based teleosemantic account of representation that we are exploring in this essay. Clearly, if that account fails, it cannot be a common explanation of the two sides of the analogy and it will still be possible to argue that the relationship between the genomic phenomena we have been considering and other representational systems is *mere* analogy. But as with the claim that the relationship between the two is *mere* metaphor, the analogy claim boils down to an argument about whether teleosemantics is a good account of representation, that is, it boils down to the main line of argument presented in this essay.

8.3 Models

We have just looked at two weaker characterisations of the relationship between nucleic acid structures and paradigmatic representational systems. Another way to look at the relationship is in terms of models. Perhaps we should not say that some genomic phenomena form part of a

representational system but that paradigmatic representational systems are a good *model* for some genomic processes.

8.3.1 Laws or models?

Most naturalistic philosophy of mind has tried to build theories of representation with a reductive program in mind. The objective is to:

- o arrive at a naturalistic account of the representation relation — that is, an account that uses only the terms and predicates of the natural sciences; and
- o show that this relation holds not just between thoughts (or inscriptions or utterances) and states of affairs — things, actions, relations etc — but also between molecular genes (or other nucleic acid structures) and states of affairs.

The states of affairs may be things (like gene products or environmental circumstances), actions (like the production of an enzyme by a neighbouring cell), or relations (like growing on an organism's dorsal surface). This is more or less my aim in this essay.

Quite a lot of people (Giere 1999) think this is the wrong way to think about scientific predicates. The idea is that scientific theories always involve idealization — a theory has to abstract from at least some features of the world to make it tractable.

- o For example, from an initial model of a ball rolling down an inclined plane you can predict that the acceleration of the ball will be: $g \cdot \sin \theta$, where g is the force of gravity and θ is the angle of the plane to the horizontal.
- o But the initial model ignores friction between the ball and the slope. So you can construct a second, more complicated model by adding a variable to take account of the frictional characteristics of the ball and the slope.
- o But the second model ignores the resistance of the air to the ball. So you can add another variable for the resistance of the air. But the third model ignores the fact that the slope is not perfectly even, etc.

One consequence of this view is that, if we take a law of nature to be a universally true and counterfactually robust generalization, all laws of nature are false because they can never capture all of the relevant features of the parts of the world they are referring to. Scientific predicates are not locked together in clean Boolean logical relations: we will, in general, not be able to define an F as something that used to be a G but changed into an H through process J , or whatever it

happens to be. Even a well worked out scientific theory does not consist of a set of laws of nature and a set of data, but a set of *models* that fit the world better or worse. Very often we will come across trade-offs between generality and realism (Levins 1966).

In general, a model-based approach to science involves three elements: a model description, a model system and a target system.

The model description is some physical representational token, or set of tokens, produced by the scientist. It could be:

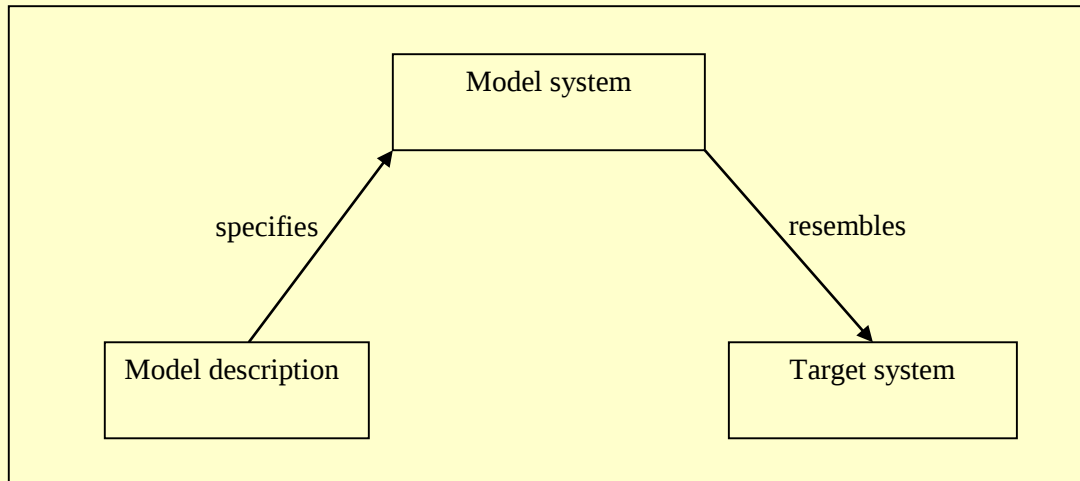
- o a set of mathematical formulae on a page, or in a computer;
- o a piece of text in a book;
- o a sequence of spoken words; and so on.

These are all physical tokens of a kind with which we are familiar. On the other hand, the model system ('the model' itself, in the vernacular), may be one of a wide range of kinds of entity. It could be:

- o a physical model, built by humans, like a model plane in a wind tunnel (Sterrett 2002, 56);
- o a system of abstract entities, like numbers;
- o an imaginary system, like an infinite population of randomly mating organisms; or
- o an organism, like *Drosophila*, functioning as a model of another species, like humans.

Models like the first three examples are, if not ubiquitous, at least extremely common in scientific inquiry. The basic structure is illustrated in Figure 14.

Figure 14: Models in science



If we try to make this schema fit the relationships between nucleic acid structures and paradigmatic representational systems like natural languages, we could say that:

- (1) the model description is a piece of English prose along these lines:
 - Suppose that:
 - a producer device (e.g. my brain, vocal chords etc) generates some intermediate items (e.g. spoken words); and ...
 - [as per Shea's characterisation of a representational system in section 3.2.7 above];
- (2) the model system is an abstract, hypothetical system involving producers, consumers, selective histories and so on; and
- (3) the target system could be any real world system that we think resembles the model system. In the case of natural languages, it would be a very large set of people and reproductively established families of linguistic forms, words, utterances, states of affairs and so on — that is, all the parts of the world and the relations among them that, according to teleosemantics, are necessary to constitute a representational system. In the case of nucleic acid structures, the target system would include the nucleic acid structures of living cells, associated cellular machinery, parts of the intra- and extra-cellular environment, together with the selective histories of the nucleic acid structures.

We can then ask ourselves how closely our two target systems resemble the abstract model system. Of course, resemblance is a slippery concept but when we are trying to evaluate resemblance between abstract model and target system in a scientific context, it seems to me that we are going to end up asking the same sort of questions as we do when we are evaluating the theory of which a theoretical definition is an element:

- o Does the abstract model (here the abstract teleosemantic model of representation) fit systems of animal signaling or human communication through natural languages?
- o Does the abstract model suggest avenues for further research? Can it be extended or varied in fruitful ways?
- o Does the abstract model generate predictions about how so far unobserved systems will behave? Are these borne out by observation?
- o Does the model fit a wide range of important cases?
- o Does the model fit with other models?

A model-based view means that we should not seek to find necessary and sufficient conditions for a system to bear representational content and then ask which systems in nature possess those conditions. In particular, when it comes to the relationship between nucleic acid structures and natural languages, we should not ask whether both fulfill a theoretical definition of a representational system but how well each of these phenomena fits a teleosemantic model of representation.

I do not think that this constitutes a fatal difficulty for my project in this essay. Even if we have to give away talk of universal laws or theoretical reduction, we can still have very good and not-so-good models. And we can use the same criteria for distinguishing between good and bad models as we use to distinguish good and bad theories of the nomological-deductive type. Just like nomological-deductive theories, models can to a greater or lesser degree generate predictions, cohere with other models, display generality and so on.

My approach in this essay has been to:

- o set out a theoretical definition of what it is for a system to bear representational content, complete with necessary and sufficient conditions for a system to do so; and
- o argue that some nucleic acid structures, as well as paradigmatic representational systems, display the necessary and sufficient conditions.

But I could equally well have described an abstract model of representation that corresponds to the theoretical definition and argue that both paradigmatic representational systems and nucleic acid structures resemble that model in important respects. We might lose the ontological satisfaction of concluding that some nucleic acid structures and associated machinery simply *are* a representational system but I think we would not lose any insight worth having into the nature of either nucleic acid structures or representational systems.

8.3.2 Non-artefactual models of nucleic acid structures

So it is possible to see the relationship between nucleic acid structures and paradigmatic representational systems in terms of the relations of both to an abstract model described by an artefact like a piece of English prose or a diagram. But we can also see the relationship, not as mediated by an abstract model system, but as a direct relationship between the target system — nucleic acid structures in our case — and another non-artefactual system — natural languages in our case — from which inferences about the target system can be drawn.

This is a model in the same sense that the fruit fly *Drosophila melanogaster* is a model for human beings. *Drosophila* is not constructed by humans as is a mathematical model or a wind tunnel.⁴⁷ This is a basic strategy in biology. Most of the publicity attracted by the human genome project was directed to the sequencing of the human genome but another important part of the project, was the sequencing of various model organisms: the bacterium *Escherichia coli*, the yeast *Saccharomyces cerevisiae*, the nematode *Caenorhabditis elegans*, *Drosophila*, and the mouse.

To illustrate an investigative approach based on naturally occurring models, Godfrey-Smith (2006) contrasts the work of Buss with that of Szathmari and Maynard Smith in investigating some of the major transitions in evolutionary history. Maynard Smith and Szathmari use a series of formal and semi-formal models and rarely refer to particular organisms while Buss talks a lot about particular organisms and derives constraints on evolutionary history from what we know

⁴⁷ The fruit flies biologists use in the lab are, admittedly, a special kind of fruit fly. They are carefully bred to weed out genetic variation so that a large group of fruit flies from the lab are much more genetically uniform than a similar sized population from the wild. But I do not know that that makes the two things very different. After all, if we're using one natural language as a model for another, we do not consult raw audio recordings of actual people talking or copies of laundry lists, we consult a cleaned-up version of the language from which the idiolects, aposiopeses and other irregularities of daily speech have been expunged.

about particular biological processes. This is the same distinction I am pointing to here: Szathmari and Maynard Smith are drawing inferences about evolutionary history by reference to models — symbol systems on a page or in a computer — that they have built, while Buss draws his inferences about an extensive set of cases in evolutionary history from a smaller set of somewhat better known cases where we have good reason to believe that the causal histories that give rise to the smaller set are relevantly the same as the histories that give rise to the broader set.

Other naturally arising models are used where it is either not feasible or not ethically allowable to build a model or conduct experiments. So, for example, an economist might use a comparable economy as a model to predict what will happen in the economy of interest or an epidemiologist might use a past outbreak of an infectious disease as a model to predict the progress of an outbreak in her community.

In this sense it is possible to see natural languages as *themselves* being a model system for a target system constituted by nucleic acid structures, their products and their activities — rather than seeing natural languages and nucleic acid structures as distinct target systems that are amenable to exploration by reference to the same model system. It could work the other way round, as well, of course — we could take natural languages as the target system and nucleic acid structures etc. as the model system. In this essay we are primarily interested in investigating nucleic acid structures, but there is clearly no reason why that should always be so. Indeed, the proponents of teleosemantic theories of linguistic meaning often appeal to signaling systems in non-human organisms as model systems for human natural languages. They use badger tail slaps, bee dances, vervet cries, frog tongue snaps and so on as model representational systems which natural languages resemble to a greater or lesser degree.

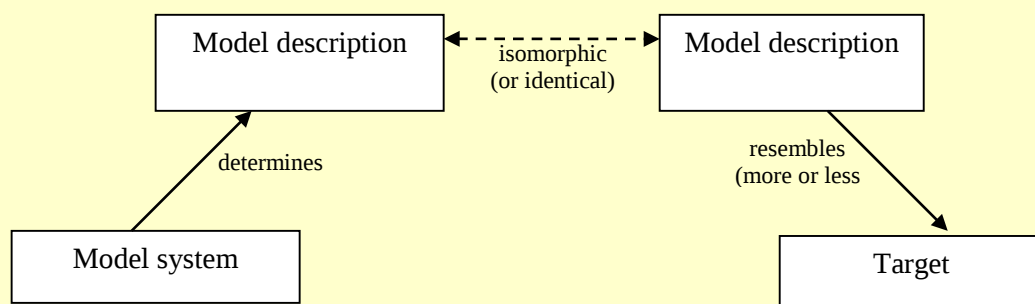
A naturally occurring model system is obviously quite different from an artefactual model system. In the case of a mathematical model or an imaginary population, the model system is designed by humans who intend it to resemble the target system. The description of the model system — the symbols on the page, the diagram, the map, or the switches in the computer — is created by human beings. The model description specifies the model system by dint of human agency and can be modified to bring the model system more closely into line with the target system. Even non-symbolic models like a scale model in a wind tunnel are built by human beings, though some of their properties of interest may not be designed by their makers: they may arise from the design of the model in ways unforeseen by the designer.

If we think that artefacts designed to represent features of the environment — thermometers, seismographs etc — can ‘inherit’ intentionality from the humans that designed them, then we may suppose that in the cases illustrated in Figure 14, the model system — a computer model, a

set of equations, a model plane in a wind tunnel, a toy train set — ‘inherits’ representational content from the representational capacities of the devices in the humans who made it.

The *Drosophila* case is different because the model system is not designed by some other intentional system (e.g. a person) to map onto a target system.⁴⁸ It is therefore described by, but not specified by, a model description. The model description does not determine but is determined by the model system. The situation looks like this.

Figure 15: Non-artefactual models



So one thing we could say is that neither molecular genes nor their products *are* representational tokens or *are* otherwise part of a representational system, but that representational systems like natural languages, can function as a fruitful model of nucleic acid structures and their activities.

In the case of a model-based relationship between nucleic acid structures and paradigmatic representational systems, I am perfectly happy to say that natural languages are a good model (in a broad sense) for molecular genes. So, for example, the relationship between speaker, utterance, hearer and object is a useful model for exploring the relationship between DNA, mRNA, the ribosome and the cellular environment. Both systems are combinatorial, arbitrary in their atomic elements, open-ended in what they can represent, and so on. And (at least arguably) linguistic relationships may be a useful model for exploring the relationship between molecular gene, trait and selective environment.

⁴⁸ Laboratory strains of model organisms are selected, often by inbreeding, for genetic uniformity: a population of laboratory fruit flies is very different from a population of wild type flies. It is therefore reasonable to say that, to some extent, the model organism is the product of human design. It is not, however, designed to resemble a particular target system.

But as in the metaphor and analogy cases, this ‘useful model’ relationship does not capture the whole of the relationship between the genome and natural language, just as it does not capture the whole of the relationship between humans and model species used to study aspects of human biology.

In the latter case, the fact that inferences about one species can be drawn from facts about another is not a matter of chance. We can draw inferences about human beings from observations of mice because both species share much of their DNA and much of their evolutionary history. We have a good explanation of the fact that mice are a good model of human beings. And the more closely related two species are, the more reliable are the inferences about one species we can draw from the other.

Similarly, we have a good explanation for the fact that natural languages are a good model for some nucleic acid structures — they are produced and consumed by devices that participate in the same functional structure and the functions in both cases are underpinned by selective processes in the evolutionary history of the relevant devices. That’s the heart of the teleosemantic story. The liver of the mouse is, I assume, a pretty good non-artefactual model for the liver of the wildebeest. Why? Because in both cases, their livers have the same biological function — to cleanse the blood — that explains why they have livers. (In this case, the connection is even closer, because the mouse livers and the wildebeest livers are members of the same reproductively established family.) A natural language is a pretty good non-artefactual model for certain genomic phenomena. Why? Because in both cases, devices in the speaker and hearer enter into the same functional relationships as the producer and consumer devices in the genetic machinery of the cell.

So it is possible to explore both nucleic acid structures and natural languages by reference to the same model system and model description, and it is possible to use natural languages as a model system through which to explore the characteristics of nucleic acid structures (or vice versa). Moreover, we have a good explanation of why this is the case.

8.4 Conclusions

Some people argue that neither nucleic acid structures nor the processes in which they participate are representational systems in the full-blown sense in which a natural language is a representational system; but that natural languages are better seen as:

- o a metaphor for the genome and genetic processes, or

- o standing in an analogical relationship with the genome and genetic processes; or
- o being more or less suitable models for certain genetic processes.

In relation to metaphors, a teleosemantic account of representational content gives us reason to believe that natural languages are no *mere* metaphor for nucleic acid structures (although it is arguable that all concepts are run through with metaphoricity).

In relation to analogy and models, I have argued that the best thing to say is that:

- o there is an analogy between some genomic phenomena and paradigmatic representational systems; and
- o paradigmatic representational systems function as fruitful non-artefactual models of some genomic phenomena; but
- o teleosemantics provides us with reason to believe that the relationship between the relevant genomic phenomena and paradigmatic representational systems is more than just analogical or model-theoretic but is in principle closer by virtue of the biological functions that they share.

Now, of course, teleosemantics could be completely misguided and I have described in section 3.2 some of the objections to it. But the important point here is that people who claim that teleosemantic accounts of representation are merely metaphorical or analogical or model-theoretical need to debunk the teleosemantic account itself before they can make their case.

9 So what?

Finally, I think it is necessary to face up to some meta questions about the issues discussed in this essay. So far I have tried to show that on a teleosemantic account of representation some nucleic acid structures possess representational content. In particular I have argued that they can represent proteins (on Millikan's account, though not Shea's), as well as features of the intra- and extra-cellular environment (on both accounts). Further, in the last section I argued that because a teleosemantic account of representation applies both to some genetic phenomena and to paradigmatic representational systems like natural languages, the parallels between the two are stronger than metaphor, analogy or useful model. But it does not necessarily follow from this that finding teleosemantic content in nucleic acid structures performs important explanatory work.

9.1 'Genuine' representational content needs to do some work

Arguing that some genetic phenomena display genuinely representational attributes is quite hollow unless we can give some important content to 'genuine': if someone does not want to call what the vervet monkeys do or what the *lac* genes do 'representation', that does not mean that they have an interesting disagreement with someone who does. We could probably get by if we called what a motor car repair manual does 'representation' and what nucleic acid structures do 'signaling' or 'representation*'.

For the application of the teleosemantic account to genomic phenomena to earn its keep, it needs to do some important theoretical work. Lumping the *lac* genes, the crying vervets and the author of a motor car repair manual together as producer devices, and lumping the ribosome, the hearing vervets and the readers of the manual together as consumer devices must aid our understanding of the living world in some way.

9.1.1 A thinner concept?

As we've seen in section 1, representation is a rich notion involving, at a minimum:

- o content — in at least some cases, an entity that represents, represents some other item or state of affairs in the external world. It manages somehow to get hooked up with some other physical state of affairs, through some kind of reference mechanism;
- o determinateness — if something is to represent, it has to represent some determinate thing, it cannot be irremediably vague or ambiguous; and

- o normativity — the concept of representation seems to require the capacity for misrepresentation. Something that represents a state of affairs in the world must represent it more or less accurately.

If our understanding of the adaptive complexity of life on earth could be served as well by a thinner notion than representation, we might think that we should make do with that. If attributing representational content to biological phenomena provides no insight that could not be gained by employing a thinner, and therefore simpler, concept, then considerations of theoretical parsimony suggest that we should prefer the simpler concept. Can we find one? Well, it certainly seems possible to see:

- o the DNA that acts as a template for the synthesis of a particular protein;
- o the mRNAs that carry the signal to the ribosome;
- o the machinery that carries out the synthesis; and
- o the intracellular environmental conditions in which synthesis is customarily initiated;

as participants in a thinner relation — perhaps we call it ‘signaling’. So we could content ourselves with saying that the synthesis of the protein signals that the cellular conditions obtain by carrying natural information about them.

The explanation of this fact could be couched in terms of evolutionary game theory. The claim would be that a stable signaling mechanism has been arrived at through evolutionary processes in which replicator dynamics have converged on an evolutionarily stable signaling strategy that reliably associates particular biological responses with particular environmental conditions (Huttegger, Skyrms et al. 2010).

This account seems to make representational claims redundant. It explains the signaling phenomena in which nucleic acid structures participate in naturalistic, evolutionary terms without direct appeal to representational concepts. The difficulty is that the simpler signaling relationship is not independent of representation, at least on a teleosemantic view.

If, as seems overwhelmingly likely, the DNA, mRNAs, and the ribosome are the products of selective processes — even if only of purifying selection that has occurred in the relatively recent

past — then they have the adapted functions that we need to establish a representational relationship:

- o it is the function of the DNA, the producer device, to act as the template for the transcription of a particular mRNA in particular cellular conditions;
- o it is the function of the mRNA, the token, to prompt the ribosome, the consumer device to perform its function, i.e. to produce the appropriate protein.

In other words, if you take a functional view of representation and an aetiological view of function, it seems hard to resist the conclusion that there is some simple kind of representation going on here. It is hard to see where to get off the teleosemantic bus, unless you endorse some different notion of function or of representation. I think the aetiological view of function is by a good measure the most convincing on offer and so I tend to think that taking a non-functional view of representation is probably the best way to debus: there are plenty of difficult challenges for teleosemantics, which I have set out in section 3.3. But if you do not take either of those options, a signaling system that has arisen through selective processes is going to display the functional structure of a simple teleosemantic system.

So if we cannot find a thinner, non-representational concept that covers the kind of signaling that we find in nucleic acid structures, are we stuck with a thick representational concept that adds little to our understanding of these phenomena but has the unwelcome side effect of finding representation in all biological processes? I believe the answer is ‘No’, and that the teleosemantic account of representation in the genome that I have presented in this essay does add to our understanding of representation in general, and of some evolutionary processes in particular.

9.2 Predictive efficacy and explanatory power

Why might extending the teleosemantic account of representation to nucleic acid processes be theoretically useful? One obvious reason is that seeing such processes in representational terms helps us predict what might happen next.

Let’s start with a trite example from animal signaling. Suppose we are watching a troop of vervet monkeys; we see an eagle approaching; we see one of the vervets turn and stare at the eagle and then we hear it emit an eagle cry. What will happen next? We know the other vervets will look into the air. Why? We might answer here that we know this because we have noted that that is what vervets do when another vervet makes an eagle cry. But — unless we are content to be stuck in a behaviourist cul de sac — why? Because the cry *means* ‘here comes an eagle’. Why?

Because it is when an eagle has been coming that the cry has in the past evoked responses from hearing vervets that have helped them survive and reproduce.

Suppose instead we are watching a platoon of soldiers; we see a helicopter approaching; we see one of the soldiers turn and stare at the helicopter and then we hear him shout ‘chopper’. What will happen next? We know the other soldiers will look into the air. Why? Because ‘chopper’ *means* ‘here comes a helicopter’. Why? Because it is when a helicopter has been coming that ‘chopper’ has evoked responses from hearing soldiers that have helped them survive and (maybe later) reproduce.⁴⁹

At the cost of labouring the point, now suppose we are watching cells in the gut of a pig; we identify lactose in the cellular environment, we observe the nuclei of some of the cells generating the polycistronic mRNA for β -galactosidase, permease and transacetylase. What will happen next? We know the ribosome and tRNAs will generate those three enzymes. Why? Because the mRNA *means* ‘there’s lactose around’. Why? Because it is when there has been lactose around that the mRNAs have evoked responses from the ribosome and tRNAs that have helped the cell (and the pig as a whole) survive and reproduce.

These important stories — stories with the same functional structure — generate accurate predictions about what’s going to happen in a multitude of situations among humans, animals, organic systems and sub-cellular structures. They explain why those things are going to happen, thanks to the selective stories underpinning the teleosemantic account of representation.

9.2.1 Function without representation?

Still, since we have been characterising representation in terms of function, it could be argued that we do not need the concept of representation at all to generate predictions about, and to explain the behaviour of, the vervets, the soldiers and the gut cells. We can tell the same story with greater conceptual economy just by using the concept of function and ignoring representation altogether. So to the question ‘Why do we know that the ribosome and tRNAs will generate those three enzymes?’, we can answer, ‘Because we know that it is the function of the DNA and associated nucleic acid structures to generate those mRNAs in response to the presence of lactose and that it is the function of the ribosome and associated structures to synthesise those

⁴⁹ This is, of course a simplification of the full story – the cry ‘chopper’ is part of a compositional natural language capable of conveying novel meanings while the monkey’s eagle cry is not – but it is close enough to do here.

enzymes on the template of the mRNAs.’ In other words, attributing representational capacities to nucleic acid structures doesn’t explain anything about the phenomena in which they figure that cannot be explained by reference just to biological functions.

On what bases might we make such a claim?

First, if the basis is the very broad one that establishing a reductive relationship between any two theories has no explanatory efficacy because it adds nothing to the explanatory efficacy of the more basic theory, that just seems wrong.

- o Using the higher level theory may allow us to formulate and test hypotheses that would not have been accessible in the more basic theory (perhaps because the limitations of human cognition mean that we simply couldn’t get our heads around the mass of detail at the lower level). In other words, using the higher level theory allows us to explain more phenomena than we would have been able to with the lower level theory alone.
- o Related to the last point, using the higher level theory may lead us to fruitful lines of inquiry that would be hard to spot if we were working only in the lower level theory. Chunking up complex statements or sets of statements in the lower level theory into simpler statements in the higher level theory can allow us to speculate about how the entities of the higher level theory are related to one another when it would not be possible to formulate the ideas in the lower level theory. Indeed, I believe this happens in the case of molecular genetics and representation (see section 9.6 below).
- o Even if working with the higher level theory does not lead to new lines of inquiry, effecting the reduction leaves us in a neater overall theoretical position. Where we previously had two unconnected theories, we now have — depending on how you look at it — one big theory or two smaller but interconnected theories. Either way, the world looks like a simpler and more intelligible place for the theoretical reduction.

Second, the claim could be a narrower one, that establishing a reductive relationship between two theories sometimes adds explanatory power to the lower level theory but that, for one reason or another, couching representational talk in terms of lower level talk about biological functions adds no explanatory power to the functional theory.

This seems just as wrong as the more general claim. For the last century, much philosophy of mind and philosophy of language in the analytical tradition has been trying to find a plausible naturalistic account of representational capacities, particularly the representational capacities of human thought and speech. We cannot help thinking that at least some thoughts and speech acts

really do represent particular parts of the physical world and representational talk is endemic in psychology, in the behavioural sciences more generally, and in daily life. But can we find an explanation of how and in what circumstances representation arises that involves only the entities, properties and relations that we customarily use to describe the physical world — electrons, atoms, molecules, membranes, cells etc. — and appeals to no other entities, properties or relations as primitives?

Teleosemantics purports to do provide such an explanation and if it does, it has significantly expanded the explanatory reach of biology in general, and functional talk in particular. It unites our ubiquitous representational talk with well-grounded naturalistic talk about biological function. You might argue that teleosemantics is rubbish, but not that, even if it is not rubbish, it adds nothing to our understanding of natural languages or human thought.

Third, the claim could be an even narrower one, that couching representational talk in terms of lower level talk about biological functions does afford better explanations of paradigmatic representational systems like natural languages and human thought, but that applying the same account of representational systems to genomic phenomena does not afford us any better understanding of *those* phenomena.

In particular, one could argue that:

- o this is because of the flexibility and indirectness of the relation between representational content and the behaviour it drives; and
- o you can only understand human action as an outcome of how humans represent the world around them, but you do not need any such representational apparatus to explain the behaviour of simpler systems like those found within the cell.

It is almost certainly true that most people's intuitions about the representational attributes of nucleic acid structures — if they exist at all — are much weaker than their intuitions about the representational attributes of sentences and utterances in natural languages. We are pre-theoretically certain that utterances have meanings so there is something to explain regardless of the theory of meaning we settle on. We are not pre-theoretically certain that molecular genes (or other nucleic acid structures) have meanings.

So in applying our teleosemantic theory of representation to genomic phenomena of one kind or another we are not trying to solve a central and longstanding a puzzle in genetics in the same way as, when we apply the teleosemantic theory to natural languages we are trying to solve a central

and longstanding puzzle in linguistics and the philosophy of language.⁵⁰ This does not, however, entail that finding representation in genomic phenomena does not help us explain them. Natural languages, animal signaling, inter-organic signaling and the kind of genomic phenomena we have been exploring in this essay are all biological phenomena; and the teleosemantic theory of representation is solidly based in evolutionary biology, so it is hard to see why applying the teleosemantic theory to genomic phenomena should have any less explanatory purchase than applying it to paradigmatic representational systems.

If we want to explain why a cell generates protein A, and we discover that A fine tunes the amount of protein B synthesised by the cell in response to chemical condition C in the cell, then we have a representational explanation ready to hand: A's action represents C to the cellular machinery that synthesises B. Certainly, these are not time-honoured and pervasive puzzles like the puzzle surrounding the meanings of humans' day-to-day utterances, but they are puzzles none the less and just as susceptible to illumination in representational terms.

Now there may come a point where the mapping between our existing, non-naturalistically-grounded theory of representation and the reworked teleosemantic theory is so poor that we think that the reworked theory is simply not a theory of representation and that we have not successfully effected a theoretical reduction. That is the point of section 7: if a teleosemantic theory that purports to characterise representation in functional terms obliges us to see representation in a host of bizarre and unintuitive places, we might have to conclude that, while the teleosemantic theory may be interesting in its own right, it is not a theory of representation. I am arguing that the teleosemantic theory of representation obliges us to see simple forms of representation in places that might seem unlikely to some people, like the genome and associated nucleic acid structures, but that this is not so much of a stretch that we can no longer see it as a theory of representation. And it is not a stretch because the systems with unexpected representational properties are of the same broad character, and have emerged from the same evolutionary patterns, as paradigm cases of representation: they are all systems under selection interacting with coordination and detection problems.

⁵⁰ Although we should remember just how pervasive representational talk is in genetics and molecular biology. Most people — philosophers or others — probably do not have compelling intuitions about the representational capacities of nucleic acid structures but it is clear that many biologists do.

9.3 A common grounding in natural selection

Explanatory reach is a good feature for a theory to possess and if we find that a single theory explains a number of different kinds of phenomena — as I believe we have in teleosemantics — then we should be pleased. But it is also nice if we know *why* our theory has such explanatory reach.

I do not think this is a trivial point. It is not automatically the case that, if a single theory explains two different sets of phenomena, we can explain why it does so. Consider penguins swimming under water and other birds flying in the air. The same theory — fluid dynamics, together with the mechanical properties of their flippers and wings — explains both how penguins swim and how flighted birds fly. A person who understood fluid dynamics and mechanical engineering would understand both how penguins swim and how flighted birds fly. In a sense, that is all there is to be said on the subject. But a theory that explains the fact that the structure of the flippers and the structure of the wings both interact in the same way with the fluids through which the birds move so as to explain the swimming and the flying, would add to our understanding of the phenomena in which we are interested. The theory of evolution is such a theory. It explains *why* penguins and flighted birds have the physical structures they do have and why they both interact in the way they do with the fluids in which they move. By explaining a theoretical commonality between two phenomena, it adds richness to our understanding of animal locomotion.

We know that a teleosemantic theory of representation can make sense of a wide range of structures and processes in humans and non-human organisms. Moreover, we have a theory that explains why teleosemantics applies to human natural languages, to animal and plant signaling, and to signaling at the nucleic acid level. The theory of evolution explains the existence of the reproductively established families that underpin teleosemantics and explains why that theory confers representational content on certain nucleic acid structures and on utterances and inscriptions of natural languages, as well as other biological phenomena, like animal signals. (In the next section we will explore a little more the coordination problems to which representational systems are one evolutionary response.)

The fact that the theory of evolution underpins the teleosemantic account of representation — in the sense that evolution explains why the teleosemantic account explains many different kinds of representation — constitutes a strong form of coherence between the theory of evolution and teleosemantics. The theory of evolution is not merely consistent with teleosemantics, nor does it just explain states of affairs that enter peripherally into teleosemantic accounts of representation; rather, it underpins teleosemantics as a whole. Teleosemantic representation is part of

evolutionary history, a kind of adaptation with a particular structure that arises as a response to coordination problems with a particular structure.

9.4 A common response to coordination problems

Moreover, such coordination problems recur at different levels of analysis. Both Millikan's and Shea's account of representation have at their core a communicative scenario in which both producer and consumer devices acquire complementary functions: it is the function of the producer to generate a range of tokens in particular circumstances and the function of the consumer to respond to these tokens in particular ways. The producer and consumer could be conspecifics, or sub-organismal systems in a single organism or, as considered in this essay, nucleic acid structures. But in each case, producer and consumer develop a communicative mechanism which in at least a critical mass of cases — enough to underpin the ascription of a biological function to the mechanism — helps both of them to survive and reproduce.

On a teleosemantic view, evolution by natural selection underpins the adapted functions of the producer, token and consumer that together constitute the functional structure of representation. But it seems natural to ask just how natural selection has been able to generate elaborate systems like:

- o the regulation of gene expression in eukaryotes;
- o the hormonal regulation of the oestrus or menstrual cycle in mammals;
- o the more sophisticated animal signaling signals like the bee dances that represent the location of food sources or the bird calls that represent the individual identity, sex and flock membership of the caller (Charrier and Sturdy 2005); and
- o human natural languages; and
- o formal languages like mathematical systems and computer languages.

The question is how these elaborate phenomena can evolve gradually from systems with no representational properties, just as evolutionary biologists try to explain how an enormously complex and finely tuned mechanism like the eye can evolve gradually from organisms with no sensitivity to light.

Bringing together population genetics and game theory allows us to answer this question, or at least to see how an answer could be developed. Consider a simple game-theoretic model (Skyrms 2010, p.10) where we have:

- o two states of affairs;
- o two populations, a population of signal producers and a population of consumers;
- o two signals available to the producers; and
- o two responses available to the consumers.

Suppose that:

- o a state of affairs arises at random, with probability of a half for each state;
- o the producer then generates a token, and generates a different token only when the state of affairs differs;
- o the token reaches the consumer, which then makes one of the two available responses, and makes a different response only when the token differs;
- o the outcome of the response affects both the producer and consumer, with the outcome depending on whether the response matches the state of affairs — Response 1 matches State 1 and Response 2 matches State 2;
- o if response and state of affairs match both producer and consumer get a positive payoff — in an evolutionary context this is an increase in the probability that they will survive and reproduce — and if response and state of affairs do not match, both get a payoff of zero.

There are only two strategies available to the producers:

- o produce Token 1 in response to State of affairs 1 and Token 2 in response to State of affairs 2 (call it strategy P_1); or
- o produce Token 1 in response to State of affairs 2 and Token 2 in response to State of affairs 1 (P_2).

Similarly there are only two strategies available to the consumers:

- o make Response 1 in response to Token 1 and Response 2 in response to Token 2 (C_1); or
- o make Response 1 in response to Token 2 and Response 2 in response to Token 1 (C_2).

Suppose that initially some proportion of producers play P_1 (and some P_2) and some proportion of consumers play C_1 (and some C_2). It turns out that, regardless of the initial proportions playing the different strategies, if the game is played over and over again, the distribution of strategies in the two populations will converge either to an equilibrium where all the producers play P_1 and all the consumers C_1 or to a situation where all the producers play P_2 and all the consumers C_2 . The interactions in equilibrium 1 look like this:

State of affairs 1 $\rightarrow$ Producer generates Token 1 $\rightarrow$ Consumer makes Response 1

State of affairs 2 $\rightarrow$ Producer generates Token 2 $\rightarrow$ Consumer makes Response 2.

and in equilibrium 2 they look like this:

State of affairs 1 $\rightarrow$ Producer generates Token 2 $\rightarrow$ Consumer makes Response 1;

State of affairs 2 $\rightarrow$ Producer generates Token 1 $\rightarrow$ Consumer makes Response 2.

In either equilibrium, State of affairs 1 is matched with Response 1, which gives both producer and consumer a positive payoff, and State of affairs 2 is matched with Response 2, which does the same. It does not matter which token acts as intermediary between the state of affairs and the response; that is entirely arbitrary.

This is a very simple model. There are more complex models where:

- o there is only one population whose members can be either producer or consumer; or
- o there are different numbers of states of affairs, tokens or responses; or
- o the probabilities of the different states of affairs differ; or
- o the pattern of payoffs varies.

And in some cases it may not be entirely arbitrary which token acts as intermediary between State of affairs 1 and Response 1 and between State of affairs 2 and Response 2: there may be some natural salience that makes it more likely that the tokens take particular roles.

Tracing through the details would take up more space than is available in this context, but hopefully this example gives a flavour of the approach. When we vary the number of states of affairs, tokens or responses, the probabilities of different states of affairs and the pattern of payoffs — and if we introduce mutation in the population or populations — we find that equilibrium signaling systems like the ones in the example will not always evolve. When we add in the costs of producing tokens and uncertainty as to whether they will reach the consumer and induce the appropriate response, we find a variety of outcomes (Skyrms 2010, §6).

Nonetheless, these theoretical results add depth to our story about how representation arises from biological functions underpinned by selective history. We do not have to content ourselves with a bare presumption that particular putative producer and consumer devices have the functions that a teleosemantic account of representation requires. We can see the emergence of those functions as a common evolutionary outcome of configurations of states of affairs, producers, consumers, responses and payoffs that have arisen throughout evolutionary history at different levels of organisation.

Divergence of interests — represented in the game theoretic models by different payoff matrices — gives rise to different representational outcomes.

In some cases there is no problem: male reed warblers use size of song repertoire to attract mates, signaling their superior fitness to female warblers. Repertoire size is a reliable and costly signal of fitness, so it is easy to see how both producer and consumer organisms benefit from this communication (Hasselquist, Bensch et al. 1996). The benefits of this kind of coordination is even clearer within organisms, where crucial sub-organismal systems share an evolutionary fate — if the organism dies they all die. In those circumstances, if different systems can coordinate their activities to respond more effectively to the environmental circumstances they face, they both benefit. But in other cases, including some cases of predator warning signals and other instances of apparently altruistic behaviour, it is harder to see how communication could have developed through natural selection.

In most genetic cases, the different systems that play the roles of producer, token and consumer in the teleosemantic pattern are part of the same organism and share its fate. So at least the patterns of negative elements in their payoff matrices look very similar: if one of them suffers a catastrophic outcome they all do. I think this suggests why most genomic representation is of the relatively simple pushmi-pullyu variety.

So there is clearly a lot we don't know about the rise of representation at different levels of biological structure. Overall, though, understanding the functional structures that give rise to

representation on a teleosemantic account as common evolutionary solutions to different coordination problems ties in our teleosemantic account more closely with pervasive structures in evolutionary history.

9.5 Evolutionary continuity

In the preceding sections of this essay I have tried to show how the teleosemantic account of representation applies, with suitable and principled variations, to a range of genetic phenomena — in other words, how nucleic acid structures can bear different kinds of representational content that correspond systematically to the kinds of tokens that arise within other representational systems. For example:

- o some nucleic acid structures bear both present imperative and present indicative content. They are pushmi-pullyu representations in Millikan's terms (see section 4.1);
- o some bear future imperative content. They are pushmi-pullyu representations where the generation of the token by the producer device precedes in time the response of the consumer device (see section 4.3); and
- o some systematically bear false present indicative information, and so deceive the genetic systems that consume them (see section 5.2).

Moreover, teleosemantics provides a coherent account of how different representational systems came to exist and how they may be divided into different classes in a principled way.

It is evolutionary theory that provides the stable underpinnings of the teleosemantic story and allows us to see the development of representational content along an evolutionary continuum that extends from the single-cued tracking mechanisms content of genomic and other (relatively) low-level biological processes to the much more flexible and sophisticated representational systems embodied in human brain processes and natural language utterances. It makes representation part of the evolutionary narrative that grounds our understanding of the living world.

Locating relatively simple genetic representational systems in an evolutionary space of systems also helps us understand how and why the kind of content they possess differs from the kind possessed by other biological systems.

For example, we can see why a relatively simple and not very accurate, representational system, like the frog's snap, has evolved and persisted. In the frog's evolutionary environment, a

representational system with limited capacities has been good enough to get by with. We could imagine a highly intelligent frog that:

- o decides whether or not to flick its tongue out by reference to a wide range of environment features (not just whether there's a black spot in the offing); or
- o keeps track of exactly how many flies it has eaten each day it has been alive; or
- o in times of plenty — stores captured flies and comes back to eat them in times of dearth; or
- o has sensitive motor systems capable of aiming its tongue snap much more accurately.

All these bells and whistles, however, would come at a cost. The frog would have to build the necessary physical mechanisms to process, store and access more sophisticated representations of its environment; this takes energy and food and diverts resources from other purposes.

If we consider cases where the producer and consumer have different, though partially overlapping, evolutionary interests, the trade-offs become more complex and the representational systems more sophisticated (Stegmann 2009). When animals of the same species are competing for resources of one kind or another, we sometimes find a hierarchy of tokens representing future behaviour on the part of the producer. For example, aggression between animals often involves escalating signaling behaviour before physical conflict occurs (van Staaden, Searcy et al. 2011).

Fighting is costly because it uses up energy, may involve injury and diverts time from other uses. So there are selective advantages to reducing the amount of fighting you actually do. Threat displays evolve because they reduce the amount of fighting that conspecifics have to engage in.

In bouts of aggressive signaling, two kinds of information are important to consumers: information about the producer's willingness to fight and about its fighting ability. In some cases, producers generate tokens that are 'unfakeable' in the sense that the token can only be produced by a particular subset of producers — producers that are big, vigorous, possessed of great stamina etc. Such tokens ('performance displays' or 'index signals') have the function of deterring the opponent from actual fighting by conveying accurate information about the aggressor's fighting ability. Other tokens may be generated by any producer, regardless of their fighting capacities. They may have some inherent cost ('handicap displays') or may be entirely arbitrary with respect to the design of the token so that the content depends on some kind of 'agreement' between producer and consumer.

There are many examples in various kinds of animals, but I'll note just one here. Song-type sharing in some species of birds appears to involve an arbitrary association between the producer mimicking the consumer's song type and his willingness to fight. Male song sparrows (*Melospiza melodia*) engage in an escalating intrusion into an opponent's territory. The aggressor first replies to his opponent's song from the boundary of the opponent's territory with a song of the same type as the opponent has just sung. He then moves into the opponent's territory and reveals himself while he continues to sing. High-end threat behaviours include singing softer songs and waving the wings, before the aggressor finally attacks the opponent (Tom, Campbell et al. 2013).

Attempting to produce a comprehensive map of representation in the living world would go beyond the scope of this essay, and given the present state of biological knowledge it is probably not possible to do so, but I hope that what I have said here at least suggests that:

- o a very wide range of different representational systems have evolved in response to different coordination problems faced by living systems, within the cell, within the organism and between organisms; and
- o seeing representational systems as evolutionary responses to a range of coordination problems helps us understand why some systems are more sophisticated and flexible while others have remained relatively simple and rigid.

9.6 Productivity

It also seems that seeing genomic phenomena as representational could prove a fertile approach for new work.

First, in this essay we have identified molecular genetic tokens that simultaneously bear indicative and imperative content. Might we be able to find circumstances in which these come apart? In the early development of *Drosophila melanogaster* it is essential for the development of a viable fly that the gene *Krüppel* is expressed only in the interior body segment (Sansom 2011, p.70). The gene is regulated by three transcription factors: *Hunchback*, *Knirps* and *Bicoid*. The factors interact so that the levels of *Hunchback* and *Knirps*, relative to the level of *Bicoid* determine the threshold between expression and non-expression of *Krüppel*. It may be possible to see the relative levels of the three transcription factors as indicative tokens that represent progress in the development of the fly and the threshold levels that trigger the expression of *Krüppel* as an imperative representational token instructing the cell's mRNA polymerase and the spliceosome to initiate transcription. There are many other examples of complex regulatory

networks where the levels of interacting transcription factors control gene expression so as to respond appropriately to the developmental status of the organism — in maize, yeast, the mouse and man, among other species (Wray, Hahn et al. 2003).

Second, we have seen that there are at least reasonably strong reasons to think that some nucleic acid structures possess future representational content. An obvious further question, is whether there is a genomic counterpart to the past tense — that is, are there nucleic acid structures that possess past representational content?

Again, regulatory networks offer interesting possibilities. We know that ‘in complex multicellular organisms gene regulation is not just a matter of turning genes on and off. It also entails fine tuning the precise level of transcription — higher or lower in different cells, higher or lower in cells of the same tissue at different stages of development’ (Hartwell, Hood et al. 2000, p.571). From what we know about feedback loops in gene regulation (Lodish, Berk et al. 2008, p.89) it seems very likely that the quantities of particular gene products in a metabolic pathway bear natural information about the history of the relevant cell and its microenvironment. Whether these quantities constitute a representational token, on a teleosemantic view, will depend on whether the molecular genes and associated regulatory regions participate in the appropriate functional structure and whether it is the function of some other system — in all likelihood a set of ligands and the regulatory regions to which they bind — to respond to the state of the pathway. This too seems to be an avenue worth exploring.

Third, it may be that some particular nucleic acid structures bear disjunctive representational content. For example, stem cells have particular characteristics that distinguish them from other cell types.

- o They are unspecialized and capable of renewing themselves through cell division, sometimes after long periods of inactivity.
- o Under certain physiological conditions they become tissue- or organ-specific cells with particular functions. When a stem cell divides, each new cell has the potential either to remain a stem cell or become another type of cell with a more specialized function, such as a muscle cell, a red blood cell, or a brain cell (National Institutes of Health 2002).

Might stem cell DNA contain *in potentia* a widely disjunctive set of instructions for different environments, such as ‘if you are surrounded by muscle cells, become a muscle cell’, ‘if no more than two of your neighbouring cells are epithelial cells and all the others are blood cells, become an epithelial cell, otherwise become a blood cell’ and so on?

Fourth, we have seen that deception ‘arms races’ can play an important explanatory role in evolution (see section 5.2). Many different organisms, particularly among the bacteria and viruses, depend for their survival and reproduction on producing tokens of kinds that participate in representational systems that have evolved in other organisms, so as to adapt the behaviour of those systems to their benefit. In this sort of case the deceived system, though it may have defences against deception, does not itself engage in deceptive behaviour.

It seems nomologically possible, at least, that there are cases where the deceiver is itself deceived by a super-deceiver. I have speculated that vaccines are such a case. If so, that is an example where the super-deceiver is a human, or perhaps better, a macromolecule that derives representational content from the intentions of the humans that design, manufacture and deploy it. But might there be comparable instances of deceive-the-deceiver that do not involve human agency?

Other variations on the theme also seem possible. We might, for example, look for cases where pairs of genomic representational systems deceive one another, as two intelligence services seek to plant double agents in one another’s organisations.

Fifth, we have seen that in some evolutionary contexts, different entities — molecular genes, ribosomes, cells, organs and whole organisms — have interests that coincide and, through natural selection, find ways of coordinating their activities so that they are able to respond more effectively to the environmental circumstances they face and both benefit.

But in other cases, it is harder to see how some representational behaviours could have developed through natural selection. So, for example, it is hard to see how an individual vervet could benefit from warning other vervets about the approach of a predator and how such a trait could arise and spread through natural selection (Fletcher and Doebeli 2009).

At the level of the molecular gene as well, we may be able to find examples where the interests of different genetic systems overlap only partially and where, as a result, their representational capacities do not conform exactly to the ‘both benefit’ model we have largely been exploring in this essay. The relationship between mitochondrial and nuclear DNA might be one possibility. Mitochondria are organelles within eukaryotic cells that probably originated as symbiotic bacteria that were completely incorporated into the host cell (Lodish, Berk et al. 2008, p.236). In sexually reproducing organisms nuclear DNA from both parents is passed to the offspring but only the mitochondrial DNA from the mother is passed on. Paternal mitochondria are largely excluded from sperm cells. A few are sometimes passed on to the fertilised egg but these are systematically degraded and destroyed (Ridley 2000 p.144). This may be an evolutionary

solution to damaging conflict between maternal and paternal mitochondria. As a result male mitochondrial DNA does not share the same fate as the nuclear DNA in the same cell: it is an evolutionary dead end. Functional relations between the two nucleic acid structures may therefore support representation where the interests of producer and consumer devices diverge to some degree (Burt and Trivers 1998).

These examples strongly suggest that our representational theory of the genome has the capacity to generate interesting extensions that warrant further work. This should hardly come as a surprise: representation is a central, complex and pervasive concept in the analysis of human behaviour and the mental processes that underpin it, so if it arises in other biological contexts we could reasonably expect it to display similar qualities in those contexts too.

9.7 So genes *are* different

Finally, discerning representation in the genome has important implications for the status of genes among other developmental resources. Molecular genes really are different from other inherited developmental resources because, as I have argued in section 7, they are by a wide margin the developmental resource with the most powerful and versatile representational capacities (setting aside cultural resources). They may not be the only such resource. For example, pheromonal inheritance mechanisms of the kind we encounter in the Mongolian gerbil and the fire ant (section 7.6) may also give rise to selective functions that fit the teleosemantic pattern. But even if other inheritance mechanisms do underpin representation, the genome is hugely more versatile in the range of states of affairs that it is capable of representing and the range of responses to which its representational tokens give rise is hugely more diverse than the responses associated with any other inheritance mechanism that may underpin representation.

This obviously does not commit us to any kind of genetic determinism or ‘genetic program’ view of development. Molecular genes are just one developmental resource among many that are essential for the survival and reproduction of an organism but on the view defended in this essay, they are different from other developmental resources because of their more potent representational capacities.

The relationship between representation and the special status of the molecular gene is an amphisbaena. On the one hand, it helps explain why molecular genes have a special status among developmental resources — because they alone underpin a powerful representational system — and on the other hand, it helps explain why representation in the genome is philosophically

significant — because it provides one reason for privileging the genome over other developmental resources.

9.8 Some modesty is called for

Still, while I think it is important that the genome possesses the representational capacities I have described earlier, we should be careful not to go overboard with the implications of the conclusions we have reached. I think there is a good case — and I hope I have presented at least elements of it in this essay — that some genomic phenomena possess representational properties as a product of their biological functions. Such representational systems form part of an evolutionary continuum extending from the simplest pushmi-pullyu representations all the way to human thought and language. So I think that representational systems in the genome and natural languages have some important things in common, but it is also important to keep these parallels in perspective. A teleosemantic account of representation licenses the recognition of only some semantic properties in genomic phenomena and the conditions set for such recognition are quite demanding, both metaphysically and epistemologically. Kay (2000) tells a detailed and absorbing story about the way some early theorists in this field went overboard in relation to the parallels between the genetic code and natural languages. To make it clear, I am certainly not claiming things like:

- o *In principle, you can read off the phenotype of the organism you are going to get from its DNA.* Development is too important and the interactions between an organism and its environment — including the maternal cytoplasm in sexually reproducing organisms and the internal environment of the organism — too complex and influential to sustain such a claim. Where this kind of talk is not just short hand, with appropriate caveats understood, it is an untenable exaggeration.
- o ‘The deciphering of DNA has revealed our possession of a language much older than hieroglyphics, a language as old as life itself.’ (Beadle and Beadle, quoted in Kay 2000, 311). I am arguing that DNA produces tokens that represent conditions in the cellular environment, but not that the representational system of which DNA forms a part is (or encodes) a natural language.
- o The representation accomplished by nucleic acid structures has a similar degree of semantic complexity to representation in natural languages. The responses of molecular genes to environment conditions are quite sophisticated and finely tuned. In some cases, regulatory networks mediate the expression of numerous different molecular genes with

different functions. So we should not underestimate the sophistication of genetic representation. But it does not seem that genetic representation has the same distinction between indicative and imperative representations that we find in natural languages or the same syntactic complexity.

Nonetheless, I do believe we should recognise genuine representation in the genome and remain open to the possibility that some nucleic acid structures have more powerful and versatile representational capacities than we currently understand.

9.9 How human beings should see themselves

Human beings are often characterised as uniquely language-using creatures. The use of language is one very important thing — perhaps the most important thing — that distinguishes human beings from other species.

Yet animal ethology has discovered a multitude of signaling systems among non-human species. Clearly these are much less complex and flexible than human languages but they also do something to blunt the edge of human exceptionalism. If we accept the arguments presented in this essay, we must see much more representation in the living world — genuine representation — and see human thought and language as the less exceptional for that.

We can no longer accept a picture in which human languages dominate a few rudimentary competitors among the ‘higher’ species of animal. Instead we must see ourselves as part of a living world of organisms in which representation of a variety of kinds — though often fairly simple kinds — is omnipresent. Human beings are not alone in their use of representation: all organisms use representational systems and produce nucleic acid tokens that bear representational content in order to coordinate their activities with their environment.

10 Conclusions

This essay has been framed around the question whether, on a teleosemantic account of representation, nucleic acid structures — particularly molecular genes in DNA and the mRNAs transcribed from them — possess representational content.

I have argued that the right answer to this question is yes, and that, if we accept a teleosemantic account of representation, there is no good reason to deny at least a rudimentary kind of representation to nucleic acid structures.

All teleosemantic views of representational content rely on some notion of function and I have discussed in brief the debate about whether the concept of function needs to be rooted in the selective history of the device under consideration. I hope I have made it seem at least plausible that function should be construed in selective terms, primarily because, as Neander argues, such a construction is firmly based in causal explanation. It both explains (in causal terms) why a particular device has a particular function and it provides us with concept of function that explains why things perform their functions.

The particular account I favour in this essay is essentially Godfrey-Smith's 'modern history' account but in most of the genomic cases we consider, any mainstream aetiological account would do. Whatever aetiological account of function you choose, it is likely to come out that the function of many stretches of DNA, 'molecular genes' in the terminology I have been using, and of corresponding mRNAs, is to act as a template for the synthesis for a particular protein in particular circumstances. Whether a particular nucleic acid sequence has a function is an empirical matter and which sequences have functions will depend on the details of selective history. If:

- o the sequence was last selected for millions of years ago; and
- o what it was selected for — what used to be its function — no longer contributes to the survival and reproduction of the organism of which the sequence forms a part;

we might say that it no longer has a selective function, consistent with a modern history account, or we might say that the original function has persisted despite its recent dormancy. We would get different results in particular cases, but I am not particularly worried about that. My point is only that in many cases, molecular genes clearly do have selective functions. Whichever precise account of function we adopt, there will be marginal cases.

The next step is to arrive at a good story about just how representational content depends on the functions of biological systems.

I argue that the most convincing model of representation is one that requires both a producer device and a consumer device to have mutually adapted functions to produce and consume representational tokens that help the consumer device survive and reproduce, either directly or by increasing the fitness of some containing organism. This is essentially Millikan's and Shea's model. Other formulations seem less plausible.

- o Attributing representational content to any system whose function it is to covary with particular states of affairs seems unrealistically permissive. We would have to attribute representation to reflexes, the dilation of the iris and a host of other biological phenomena. This in itself is not a conclusive argument but it does suggest that something is missing in this kind of account. In particular, it is missing the communicative aspect of representation. Paradigmatic representational tokens are used in some way by some consumer device. A covariation story misses the distinction between the producer, the token and the consumer which is essential to paradigmatic representational systems like natural languages and systems of animal signaling.
- o Papineau's account of representation relies on a distinction between indicative and imperative representational tokens, i.e. roughly, beliefs and desires. The content of a belief is derived from the function of the imperative representations with which it is its function to interact. This has its strengths but it is rather hard to see how we can distinguish states with representational functions, like beliefs and desires, from states with non-representational functions: nature provides us with many instances of devices with adapted functions that do not seem to be representational, and it is not clear how Papineau can distinguish in a principled way between representational and non-representational adapted functions.
- o A radically consumer-oriented approach to the problem, as adopted by Jablonka, also seems to run into difficulties. If we say that representational content is generated when a consumer device interprets some input so as to generate a response that usually helps it survive and reproduce, we end up blurring the difference between natural information and representational content. If a hunter interprets an animal track in such a way as to help her survive and reproduce, the consumer-centric approach says it conveys information, but it surely does so only in the sense of natural information: it is not the function of the animal track to generate a response in the hunter.

- o In the end I think that Millikan's teleosemantic account of representation is probably the best around. For representation to arise, she requires that a producer device has the function of producing a token and that a consumer device has the function of producing a state of affairs onto which the token will map, in the sense that a 'critical mass' of tokens and states of affairs have been correlated in a way that has aided the consumer device (and its ancestors) to survive and reproduce. Shea sets out a more demanding version of Millikan's formulation on which (a) the content of a token must be the evolutionary success conditions with which the ancestors of the token have been associated and (b) the producer device must be able to produce a range of tokens to which the consumer can respond. I prefer Millikan's more permissive account, although I believe that both Millikan's and Shea's account are useful and, in most of the genomic cases considered in this essay, will give the same answers as to function and content.

With this framework in place we are a position to ask whether it makes sense to say that nucleic acid structures possess representational content and to get a bit more precise about what that content might be.

We consider three kinds of representational content that nucleic acid structures might possess.

First, a nucleic acid structure, particularly a coding region of the DNA sequence, could represent the protein for whose synthesis it acts as a template. The idea has some intuitive appeal because of the very linguistic look of the genetic code, the map of correspondences between triplets of nucleotides on the DNA and the amino acids for whose synthesis those triplets act as a template. But when we get to the details, it turns out that whether or not we find representational content depends on the fine structure of our account. Millikan's story allows us a little more latitude in identifying representation than Shea's because her account does not require that the content of a token be the evolutionary success conditions with which the ancestors of the token have been associated. So it turns out that an mRNA that acts as a template for the synthesis of a particular protein meets her characterisation of an intentional icon. Shea's somewhat more demanding formulation requires that the token represent the evolutionary conditions in which it has evoked an adaptive response from the consumer device, so it cannot represent the protein, which is response of the consumer device itself.

Second, a nucleic acid structure could represent a trait to which it makes some decisive causal contribution. People often speak fairly loosely about the gene 'for' some trait even though in the huge majority of cases, differences in more than one gene, frequently very many, normally produce differences in any given trait. We can make more precise what we mean by a gene for a trait, by stipulating that the molecular gene's function must be to generate a trait, by virtue of its

having been selected for so doing, but it does not follow that a gene for a trait *represents* the trait. We need to decide whether we can find a functional structure linking some producer device, the molecular gene, and a consumer device in a way that meets the requirements of the teleosemantic model. I cannot see a way to do this. The problem is that it does not seem possible to specify a consumer device in a plausible way. Even if we think that the producer of the molecular gene is the gametes of the parents (in a sexually reproducing organism), it seems that the consumer could only be a congeries of environmental and genetic developmental resources that surely has no selective function.

Third, a nucleic acid structure could represent conditions in the cellular environment. This I think is more plausible. There are many examples where a nucleic acid structure in an organism's DNA responds, often through complex regulatory pathways, to particular conditions by generating an mRNA token that triggers the synthesis of an protein that helps the cell (and the organism of which it is a part) deal successfully with those conditions. In such cases we can identify producer and consumer devices, although admittedly they are relatively large complexes of nucleic acid structures and associated cellular machinery. It is nonetheless very likely that these systems have been selected for their capacity to participate in the producer-token-consumer interactions that allow the cell to respond successfully to the prevailing conditions in its environment. So when such a system tokens an mRNA that acts as a template for the synthesis of an appropriate protein, the mRNA fulfils the role of a token that represents the cellular conditions.

It seems clear that most nucleic acid structures that bear representational content are what Millikan calls pushmi-pullyu intentional icons. They are neither indicative nor imperative, but both at once. Their function is both to map onto the cellular conditions to which they are a response and to adapt the activities of the cell to those conditions. The response is temporally immediate and the token does not participate in any inferential processes in order to evoke the response.

However, it seems that in at least a few cases, genomic phenomena display more sophisticated representational capacities.

- o Genetic clocks control biological processes in pretty much all multicellular organisms and can be synchronized ('entrained') so as to ensure that particular processes coincide with future conditions in the cellular (or broader) environment. Under our teleosemantic account of representation, these processes represent the future conditions that they are meant to help the organism deal with.

- o A teleosemantic account of deception also seems straightforward enough. Suppose we have a family of producer devices and a family of consumer devices participating in a representational relationship of the usual teleosemantic kind. Then suppose we have a second family of producer devices whose function it is to produce tokens of the same kind as the first family of producers but in circumstances where the responses of the consumer devices benefit the second family of producers rather than the consumers themselves. This is a plausible account of deception in a teleosemantic framework. In practice, at the genetic level, we find many examples where one organism deceives another by using the genetic machinery of the second organism for the first organism's benefit. Bacteria and viruses both mimic genetic signals usually generated within the host organism to hijack its genetic machinery to the parasite's benefit.

Fourth, a nucleic acid structure might represent conditions in the extra-cellular environment, either contemporary conditions to which the genome responds by gene expression, or conditions in the evolutionary environment in which the structure has been selected for. The first alternative follows the same pattern as representation of conditions in the cellular environment: in some cases we *can* identify the kind of functional producer-token-consumer that allows the consumer device to respond successfully to the extracellular environment. The second alternative runs into the same problem as we encountered when we considered the possibility of a nucleic acid structures representing a trait with which it is associated. It does not seem possible to specify a consumer device in a plausible way. Our teleosemantic story requires the token to represent some sort of conditions that the consumer device can respond to, or in the case of an imperative token, some state of affairs that the consumer device can bring about by an appropriate response. The evolutionary environment in the ancestral past of the consumer device is not conditions that the consumer can respond to.

Given this framework and these conclusions about when representation arises in the genome, we explore a key characteristic of the genome that is crucial to the scope of its representational capacities, that is, the compositionality of the genomic system and the arbitrariness that underpins it. Like natural languages, protein synthesis depends on a small set of arbitrary elements — the four nucleotides that make up DNA and RNA — that allow the composition of an almost unlimited set of larger units such as molecular genes, regulatory regions and operons. Both are digital systems that produce and re-identify tokens from a fixed set of types. Both allow the construction of much longer strings whose representational content differs systematically with the elements that make them up and the order in which those elements are arranged.

And in both cases, the physical makeup of the elements is quite arbitrary. There is no chemical or physical reason why different codons could not have become assigned to different amino acids. Indeed, slightly different variants on the standard genetic code do occur in some yeasts, bacteria and in mitochondrial DNA. Both natural languages and the genetic code seem to be the product of historically contingent developmental processes.

The kind of teleosemantic story I tell faces a long list of objections but in this essay I discuss only three of them in detail.

First, it can be argued that if nucleic acid structures bear representational content, many other developmental resources must do so as well. Of course, you could accept this conditional and its antecedent and simply put up with lots of representation cropping up in odd places in the biosphere. My position is that, so far as they have been established, the facts relating to developmental resources other than the genome do not, by and large, support the claim that other developmental resources bear content in the same way as nucleic acid structures. Most other resources lack the selective history necessary to underpin biological functions and those that have functions mostly do not appear to have the right functional structure to generate representation under a teleosemantic account. The most likely candidates are chromatin markings on DNA, some environmental effects that give rise to inherited characteristics, and some behaviour of symbionts that have co-evolved with their hosts.

Second, there are a number of ways to argue that the resemblances between genomic phenomena and paradigm representational systems are not sufficient to establish that the genome bears representational content.

- o It can be argued that in the context of the genome, representational content is no more than a metaphor and that it is not literally true that genomic phenomena bear representational content. But this really boils down to whether you think that (a) a teleosemantic account of representational content is a good one and (b) that under such an account some nucleic acid structures bear representational content. If you think (a) and (b), you can legitimately hold that it is literally true that some nucleic acid structures bear representational content. The claim that representational content in nucleic acid structures is 'just a metaphor' does not seem to contribute any independent arguments against a teleosemantic position.
- o It can be argued that while there is an analogy between some nucleic acid structures and paradigm representational systems, this is not enough to establish that nucleic acid structures actually bear representational content. Again, this just seems like another way

of saying that there is something unsatisfactory about a teleosemantic account of content or that, while that account is acceptable, it does not fit the facts relating to genomic phenomena. My claim is that the analogy between some nucleic acid structures and the tokens of paradigmatic representational systems like natural languages is sufficiently strong to support the claim that both are representational because the analogy is underpinned by the one evolutionary story that confers representational content on both of them.

- o It can be argued that while paradigmatic representational systems can be useful as a model for some nucleic acid structures that does not mean that they both bear representational content. There are two ways of taking this. If you think that all science is model based, and that mathematical models, theories described in prose, wind tunnels, model organisms and computer models, are all just more or less useful models of the parts of the world they are used to explore, then my response is that the relationship between some nucleic acid structures and the tokens of natural languages is as close as it can be on this view of science. If you think that science involves the use of models but some models are so preferred to others that we can privilege them as 'true' in some way, my response is that, because of the virtues of the teleosemantic account and the functional correspondences between some nucleic acid structures and the tokens of paradigmatic representational systems, we should regard paradigmatic representational systems as a preferred model in relation to some nucleic acid structures.

Third, and more fundamentally, it can be argued that discerning representation of a rudimentary kind in the genome serves no explanatory purpose and, in particular, that it adds nothing to a description of the functions that underpin representation on a teleosemantic view. I do not agree with this.

- o Representation is a crucial and widespread phenomenon in human life. If we come up with a good account of it couched in terms of biological function and that account extends to genomic phenomena, it seems to me we have greatly increased the coherence of our world view.
- o A representational account of the genome presents us with a range of intriguing questions for further work: it generates a research program. Can we go beyond the pushmi-pullyu representations on which this essay is focused and find genomic representation that is clearly indicative or imperative but not both at once? We have found instances of gene expression representing future conditions; might we be able to

find instances where genomic phenomena represent the past? In both these case the fine tuning accomplished by regulatory networks offer interesting possibilities.

- o We can also look for disjunctive content borne by genetic tokens, for variations on the theme of deception among genetic systems and for systems where communication between producer and consumer devices falls somewhere between full blown cooperation and outright deception.
- o A teleosemantic account of representation, including representation effected by nucleic acid structures, gives a united account of a continuum of representational systems, ranging from simple pushmi-pullyu systems to more complicated systems of communication among the higher primates and the more and less sophisticated representational systems employed by human beings.

Finally, genetic representation is important because it redefines humans' place in the representational world. We often pride ourselves on being the only species that uses language. Yet the evolutionary story about how we got here and how our capacities arose suggest that we are all of a piece with the rest of the living world. The story we have told in this essay extends that continuity to representational capacities. We humans have the most flexible representational capacities that we yet have encountered — *pace* the whales — and we may reasonably regard human natural languages as the most complex, powerful and adaptable representational systems that have so far arisen on this planet. But we may not believe that the human voice is alone on earth. It is one of many millions, produced by and within organisms at all levels of complexity, in all kingdoms of biota and in all periods in the history of life.

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