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# Mechanistic Information and Causal Continuity[1]

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(Forthcoming in Phyllis McKay Illari, Federica Russo, and Jon Williamson, eds., *Causality in the Sciences,* Oxford University Press.)

**i. Introduction**. Since the middle of the 20th century neuroscientists, evolutionary theorists, molecular geneticists and other biologists, have talked as though *information* and *information flow* are important explanatory notions. However, some influential recent literature in philosophy of science disagrees. Paul Griffiths says that although

> …there is a genetic code by which the sequence of DNA bases in the coding regions of a gene corresponds to the sequence of amino acids in the primary structure of one or more proteins,… the rest of 'information talk' in biology is no more than a picturesque way to talk about correlation and causation. (Griffiths [2001] p. 395)

In conceding that 'there is a genetic code' all Griffiths commits himself to is a simple (though degenerate) mapping relationship between sequences of DNA codon bases and amino acids on protein precursors. In rejecting the rest of 'information talk' he denies that explanations and descriptions of biological phenomena couched in terms of information flow can tell us anything that cannot be said simply by talking about causes and correlations. He endorses Sahotra Sarkar's claim that no matter how much working biologists talk about information

> …there is no clear, technical notion of "information" in molecular biology. It is little more than a metaphor that masquerades as a theoretical concept

[1] We began work on the ideas in this paper a long time ago in conversation with Lindley Darden to whom we are greatly indebted for this and for helpful criticisms over the past several years. We are also indebted to Megan Delehanty, Fidel Mejia, Jim Woodward, Jack Vickers, Ken Schaffner and to audiences who discussed earlier versions and related talks at the University of Pittsburgh, the University of Maryland, the University of Calgary, the College of William and Mary, to Emi Iwatani, Jason Byron, and other students in a seminar we taught on mechanistic explanation, Anjan Chakravartty and an anonymous referee for helpful suggestions, and to Deborah Bogen.

> and ...leads to a misleading picture of possible explanations in molecular biology. (Sarkar [1996], p. 187)

We agree with the biologists.[2] Ideas about information have been and continue to be important to the development and articulation of exemplary explanations of some fundamental biological phenomena[3].

Standard biology textbooks invoke information to answer questions about biological processes they seek to explain. We maintain that information talk in biological explanations cannot always or often be satisfactorily replaced by descriptions of correlations and non-informational causal connections. Crick's 'On Protein Synthesis' is a classic illustration (Crick [1958]). Although we don't agree with much of what Crick says about information flow, we follow him in thinking that the continuities of some fundamental biological processes do depend upon information storage and transmission. This paper's main examples of this are DNA expression and a sensory-motor reflex which functions to move leeches away from things that press against them.

The poet Frank O'Hara described the development of his poems as taking the form: I do this, I do that (http://findarticles.com/p/articles/mi_m1248/is_2_88/ai_59450177/).

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[2] The debate over whether *information* is a helpful concept in biology often focuses on the role of genes and genetic expression in evolutionarily significant processes involving the emergence and transmission of the adaptive effects of heritable traits. (See Smith [2000], Sterelny [2000], Godfrey-Smith [2000], Sarkar [2000], Smith [2000a]). A further focus is on the question whether genotypes and phenotypes are coupled closely enough to support controversial versions of genetic and evolutionary determinism. We agree with Griffiths' skepticism about the idea that "genes" code or transmit information about phenotypes, but we disagree with him about the role of information in the synthesis of protein precursors and in some other biological processes.

[3] Sarkar grants that the concept of information can be play a useful heuristic role 'in the construction of some scientific entity' but denies that it 'explicitly occurs in that entity'. (Sarkar [2000] p. 209) If this means that it was useful for biologists like Crick to think about information in constructing their theories, we agree. We don't know how Sarkar distinguishes ideas which occur explicitly and do real scientific work from those that don't. But we maintain contrary to Sarkar that over and above its heuristic value *information* does do important explanatory work. Furthermore we maintain that information transmission plays a causally significant role in the biological processes it is invoked to explain.

The continuity of a causal process might be analogously described by saying that this causes (or contributes to the production of) this, and that causes (or contributes along with such and such other factors to the production of) that. Frank O'Hara style causal descriptions can tell us all there is to know about how a number of biological processes develop from step to step. As we discuss in §iii and §iv, the Krebs cycle is a case in point. But they fail to capture important facts about connections between the steps that take the mechanism of protein synthesis from the transcription of a segment of DNA to the production of a polypeptide string of amino acids. The same holds for connections between the steps of the leech reflex whose operation is initiated by something pressing on the organism's body and completed (if all goes well) by muscle contractions that move the leech away from the source of the pressure. In cases like these, causal factors at work in the initial steps of the process exert a strong influence on the development of the process and the result that completes it. The kind of influence they exert distinguishes these processes from processes whose continuities can be explained without appeal to information. In the remainder of this paper we set out the notion of information that we take to be appropriate to the explanation of the continuities of DNA expression, the leech escape reflex and other biological mechanisms whose initial causal factors make similar contributions to their continuities.

**ii**. **Processes and mechanisms**. The processes we consider in this paper—informational and non-informational alike--are operations of mechanisms in the sense of Machamer, Darden, and Craver (MDC) [2000]. An MDC mechanism is an arrangement of entities which engage in an ordered sequence of activities. The activities that entities engage in move the mechanism from an initial or start-up condition through one or more steps[4] to a result that marks the end of its successful operation. The activities move the mechanism forward by initiating, sustaining, modifying and damping the activities of other entities and in some cases, by incorporating or producing new component entities and eliminating or modifying preexisting ones. Mechanistic explanations answer

[4] Steps are individuated in terms of causal sub-processes. We lack space to say more.

questions about the entities, the activities and the parts they play in producing results to be explained.[5] As MDC observe, ideal mechanistic explanations

> …exhibit productive continuity without gaps from the set-up to termination conditions. Productive continuities are what make the connection between stages intelligible. (Machamer, Darden and Craver [2000] p. 3)

All mechanisms

> ...have productive continuity from one stage to the next…[such that] entities and activities of one stage give rise to the next stage…but few mechanisms have information flow through multiple stages of the [operation of the] mechanism. (Darden [2006] p. 283)

Whether information ought to be invoked to explain how a mechanism operates depends in part on the interpretive stance taken by its investigators. For example, molecular biologists found it useful to interpret certain features of DNA expression in terms of information when biochemical interpretations proved unfruitful (Darden [2006] p. 280 ff.). But the correctness of their explanatory claims depends on facts about the makeup and the operation of the mechanism that obtain independently of interpretive or explanatory strategies. One crucial difference between the operations of mechanisms that do, and those that do not involve information turns on what we call the *reach* of causal influences exerted by initial factors. To illustrate what this means we will sketch some differences between DNA expression (an informational process) and the Krebs cycle (a non-informational process).

A second crucial difference is that the continuity of an informational mechanism is a function of its teleological structure. Informational biological mechanisms operate for the sake of achieving or promoting goals of the organism (or one or more of its component subsystems) to which they belong.[6] Information, as we think of it, consists of the causal

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[5] For details see Machamer, Darden, Craver, [2000] passim, Darden [2006] pp. 1-12, 13—98, 271—312.

[6] Information may figure in the operation of artificial as well as natural mechanisms. The goals that the mechanisms (help) satisfy may be natural or imposed on them by humans

influences that achieve or promote relevant goals. When the system is in good working order and the mechanism functions as it should, the information an entity or activity transmits (i.e., the causal influence it exerts on other components of the mechanism) contributes to the production of a result that achieves or promotes the goal for the sake of which the mechanism operates. We discuss this below in §vi. But mechanisms are subject to different kinds of malfunction. In some malfunctions—e.g., where interfering factors keep the mechanism from operating or from moving all the way to its final step--information plays no significant role. In others, e.g., the expression of mutant DNA responsible for cystic fibrosis, information contributes to malfunction by moving the mechanism toward a result that prevents the achievement of its normal goal. We discuss this in §vii.

**iii**. **Reach**. To illustrate the notion of reach, consider how DNA codons direct the selection and arrangement of amino acids to form protein precursor polypeptides. The production of amino acid strings begins when the bases on a DNA segment bind weakly to their complements[7] to produce a string of nucleotides which is then detached to form a strand of pre-mRNA. Later the pre-mRNA strand is cut and spliced to produce a strand of mRNA. Still later, amino acids attached to ribosomes decorated with the complements of mRNA bases are carried and attached to mRNA strands. The bases to which ribosome bases bond are the complements of codon bases on the DNA segment that is expressed. As a result the amino acids carried by the ribosomes are arranged on the polypeptide to stand in the same spatial relations as the bases on the DNA codons. Because the bases bind weakly only to their complements, DNA codon bases exert a direct influence on the

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or other organisms that use them. We focus on natural mechanisms and ignore what they do to satisfy the goals of human and other users. For example, what we have to say should apply to fermentation as a metabolic process in yeast, but not as a step in intentionally producing wine.

[7] For example, cytosine bonds weakly to guanine, and adenine bonds weakly to thymine or uracil (Alberts et al [2002] p.302).

production of pre-mRNA and a strong indirect influence that extends to the products of subsequent steps of polypeptide construction.

To make the notion of reach more vivid, compare the extensive influence of DNA codon bases on polypeptide construction to the weak influence the oxaloacetate molecule that interacts with other chemicals to begin each round of the Krebs (citrate) cycle.[8] Each round of the cycle consists of eight chemical reactions. Each reaction uses chemicals supplied by a number of different mechanisms to produce a molecule that serves as a substrate for the next step in the cycle. Many of the mechanisms that supply chemicals to interact with the substrates operate more or less independently of one another. And they are part of the Krebs cycle only to the extent that some of its byproducts contribute to the production of energy carriers and other vital molecules needed to sustain their operation. Thus, none of the substrates of Krebs cycle reactions exert an influence of any considerable reach on subsequent steps.

In slightly more detail, a number of different chemicals from different sources enter into the first two steps of the cycle. Oxaloacetate (the substrate for step one) does little by itself to limit the number of results that can be produced in step two. Moreover, the influence of oxaloacetate diminishes from step to step as the new substrates are produced. For example what goes on in step five diagramed below depends upon the chemical behavior of succinyl-CoA, the substrate supplied by step four, together with additional chemicals (including GDP, water, inorganic phosphate molecules and synthetase enzyme, for example) that are made available by interactions that do not belong to the cycle itself. **Fig. 1** here.

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[8] The production of citrate from oxaloaetate is customarily singled out as the first step of the cycle because of its place in the metabolic process that takes the organism from food intake and breakdown to the production of physiologically useful energy carriers. (For details see Alberts, et al. [2002] pp. 95—108 & 126-7.) But treating any other step as the beginning of the cycle would make no difference to what we have to say here.

These chemicals work together to produce succinate, the substrate for step six. The chemical makeup of succinyl-CoA places some constraints on what molecules can be produced at subsequent steps. But these constraints are so weak that a great many different interactions producing a great many different molecules would occur if different enzymes and reactants were present instead of the ones that are normally available to help move the cycle forward. According to Peter Wipf

> For the 9 small molecules[9] involved in the citric acid cycle, any good chemist could draw you upwards from 200 different reactions giving different products from the specific enzyme-mediated processes. For somebody trained in the art of synthesis, the number would go up to maybe 5,000. (Personal correspondence)

The burden of deciding which of these molecules can be produced falls mainly to the influence of the reactants and enzymes that various mechanisms provide after the completion of step one.

We characterize *reach* in terms of strength and independence of influence as follows:

Strength of influence. The strength of an entity's or activity's influence depends on how many alternative results it rules out or renders significantly improbable in subsequent steps in the operation of the mechanism.[10] The more downstream outcomes it leaves open, the weaker is its influence.

Independence of influence. This is a robustness condition. The less a factor's influence depends on background conditions over which it has no control, and the greater the range of different background conditions under which it can produce or contribute to the production of the same downstream results, the more independent is its influence on

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[9] The nine small molecules are the substrates that begin each step together with acetyl CoA.

[10] By 'alternative results', we mean outcomes which are physically, chemically, anatomically and physiologically possible rather than outcomes which are just logically possible or conceivable from the vantage point of the armchair from which philosophers think about "nearby possible worlds." A detailed account of what this amounts to must await a further paper.

the operation of the mechanism.[11] Because bases bind to their complements independently of the background conditions under which binding occurs, the influence DNA codons exert on the construction of RNA strands and polypeptide chains is considerably more independent than the influence that the oxaloacetate molecule exerts on the production of molecules in the Krebs cycle.[12,]

Reach. The reach of an entity's or an activity's influence depends on how many steps are strongly influenced by it and how independently it influences them. It should be clear that the reach of the influence exerted by DNA base sequences extends to the order of the amino acids. (We discuss the reach (strength and independence) of initial causal factors in the leech's pressure escape mechanism below in §v and note 20).

While the reach of initial factors is important, it is not sufficient to distinguish informational from non-informational continuities. Consider the example of a very smooth block that slides down a very smooth plane in response to a gentle tap, strikes a domino at the bottom of the incline and knocks it over.[13] Absent interfering causes, the tap that starts it on its way exerts a strong and independent influence on its direction and velocity at every step of its slide and on the fall and final position of the domino, but this is by no means an information system. A Frank O' Hara style description of the relevant causal sequence suffices to explain what happens from the tap to the domino's falling over and coming to rest. Similarly, there is no information in the process that takes a drinker from alcohol ingestion to intoxication even though the alcohol exerts an influence

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[11] We distinguish independence from strength because a factor, X, that influences the production of results at a number of different steps may do so only in connection with different factors, $y_1,\ldots.y_n$, at every step. If the y factors decide which results are produced and X has no control over which of the y are available at any given step, X's influence can be strong but not independent.

[12] We are indebted to Jim Woodward for conversation on this topic and for making available a draft of a paper in progress on causality in biology that develops a related idea.

[13] We stipulate that the block, the incline, and the domino have not (as perhaps they could have) been incorporated into some sort of Rube Goldberg mechanism whose proper functioning depends upon the way the domino falls.

of great reach. Furthermore, the notion of reach applies only trivially to causal influences in mechanisms that move from start up to end states in a single step. The teleological structure of DNA expression and the leech reflex is what distinguishes them from the falling dominos.

**iv**. **Teleological structure and reach differentiate the Krebs mechanism from informational mechanisms**. To recapitulate, we've seen that the mechanisms responsible for the leech reflex and for DNA expression operate to satisfy needs for the organisms they belong to. These mechanisms are activated by factors that indicate what results they must produce in order to serve their purposes. Thus in response to pressure, sensory neurons engage in activities whose reach extends far enough through the operation of the reflex mechanism to direct it toward the production of teleologically appropriate muscular activity. A crucial difference between the pressure escape reflex and the Krebs cycle is that in comparison to the factors that set it in motion, the factors that begin the Krebs cycle have very little influence on what happens downstream. But reach doesn't explain why the operation of the block-incline-domino mechanism is non-informational. The tap that starts the block on its way toward the domino has a great deal to do with the fall of the domino. With regard to mechanistic information, the crucial difference between the escape reflex and the block-incline--domino mechanism is teleological. The block-incline--domino mechanism does not belong to a system with goals for the block to promote by knocking over the domino. DNA expression differs from the operation of the block-incline-domino mechanism in the same way—by virtue of operating to help satisfy needs of the organism.[14]

Someone will want to know how we can accommodate what we've just been saying to the fact that the Krebs cycle benefits organisms by producing energy carrying GTP and NADH, and other beneficial molecules including the precursor of energy carrying ATP.(Alberts et al [2002] pp. 92, 102, 106). It is arguable that this is why the Krebs

[14] See previous note. We are indebted to Ken Schaffner for pointing out how often biologists describe biological functions in terms of needs. For just a few examples see Alberts, et al [2002] p.380, and Lewin [1994] p. 418.

cycle survived natural selection. We are indebted to Lindley Darden for commenting that philosophers who identify the goals of biological mechanisms with functions for which they were selected might conclude from this that the Krebs cycle operates for the sake of supplying the organism with certain vital molecules. But even so, biologists and biochemists seldom invoke information to explain how the cycle operates as they do in connection with DNA expression. According to us that is as it should be because the molecules that figure in its first step have next to no influence on the direction the cycle takes in moving toward the result that marks its final step. As we said, reactants that originate outside of the mechanism do much of the work in selecting products to be produced, e.g., at steps 5 through 8 of the cycle. As a result, the strength and independence of the influence of oxaloacetate molecules diminishes to relative insignificance as the cycle moves on.

Furthermore, although the Krebs cycle plays a teleological role it does not have the kind of teleological structure that is required for a mechanistic informational process. When all goes well the operations of the leech reflex and the DNA expression mechanisms end with the very result whose teleological appropriateness was indicated by entities and activities belonging to their first steps. By contrast, the oxaloacetate molecule whose production completes the Krebs cycle benefits the organism only as a substrate for the first step of its next round. In contributing to the continuation of the cycle, the benefit oxaloacetate provides is no different from that of the products of every other step. The vital molecules the Krebs cycle produces for the organism are released as byproducts before the cycle reaches its final step.

Jason Byron objected in discussion that the Krebs cycle resembles DNA expression more closely than we acknowledge. The molecules that interact with oxaloacetate to begin the cycle are obtained from carbohydrates whose ingestion is typically increased by hunger which indicates a need for energy carried by GTP and NADH. Thus if hunger tracks energy closely enough, and sugars are metabolized sugars efficiently enough, hunger could regulate the rate at which the Krebs cycle mechanism produces needed

energy carriers.[15] But this doesn't imply that the Krebs cycle has the teleological structure exemplified by DNA expression and the leech reflex. Over and above the fact that GTP, FADH, etc., are byproducts rather than results completed by the cycle's final step, we've seen that the molecules that set the cycle in motion don't even do much to direct the cycle toward the production of its beneficial byproducts. Thus Frank O'Hara style causal accounts can tell us all we need to know about the continuity of the Krebs cycle. But trying to explain the continuity of polypeptide construction or the pressure escape reflex without appeal to the goals their mechanisms serve, and connections between their goals and the control that first step factors impose on their operation would be like trying to explain the continuity of a chess game without reference to the object of the game or the influence of tactical considerations.

**v**. **Mechanistic information**. We use the term 'mechanistic information' in connection with the notion of information that we think is appropriate for explaining continuities in the operation of goal directed mechanisms that Frank O'Hara descriptions cannot account for. We turn now to our characterization of mechanistic informarion, beginning with the first of several comparisons to other notions of information.

As Lindley Darden explains, Crick believed that information flows from DNA to direct protein precursor construction and that information flow consists of pattern replication. Amino acid strings are encoded after the manner of Morse code messages by sequences of DNA codon bases (Darden [2006], p.282-3). The pattern into which these bases are arranged is instantiated on RNA strands by codons whose bases are the complements of the basis in their DNA codon counterparts. According to Crick the same pattern is replicated from step to step until its final instantiation--a string of amino acids that will be folded to complete the protein encoded in the DNA segment.[16] We agree with Crick in

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[15]. For the sake of the argument, ignore people like us who eat when they have no physiologically good reason to do so. Byron's example was an athlete who eats after exercise in response to hunger caused in part by energy depletion.

thinking of DNA information in terms of '…the specification of the amino acid sequence of the protein' that has been selected for synthesis (Crick [1958] p.144; Cp.p.153). But we disagree with his ideas about information flow. As we said, DNA segments are expressed in order to supply the organism (or one or more of its subsystems) with proteins it needs. So-called housekeeping genes are expressed more or less continuously to provide proteins the organism needs at all times, e.g., to support cell metabolism. Other DNA segments are expressed occasionally to satisfy temporary needs for proteins to support special functions (e.g., muscle contractions and relaxations in the execution of a dance step). The construction of a protein precursor actually does begin with the replication of a pattern; a DNA segment is selected to serve as the template for the production of a strand of pre-mRNA whose nucleotide bases stand to one another in the same spatial relations as their DNA complements. Anti-codons are sequences of nucleotides. Like codons, each anti-codon is a sequence of three nucleotides. Anti-codon nucleotides complement and stand in the same special relations to one another as those of the corresponding DNA codons. Thus pre-mRNA anti-codons instantiate the same pattern as codons. But pre-mRNA is cut and spliced to produce mRNA and in the process molecules standing in between anti-codons are removed. As a result anti-codons that were spatially separated on the pre-mRNA strand are adjacent to one another on the mRNA strand. Suppose CUCAGCGUUACCAU are the bases on a string of anti-codon nucleotides that comprises a part of the mRNA strand. As it stands this string could function as any one of several different sequences of anti-codons, each of which codes for a different arrangement of amino acids.[17] Because the string is ambiguous with regard to

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[16] For simplicity we ignore the influence of DNA bases which do not encode polypeptide amino acid sequences but contribute instead to the production of non-coding RNA molecules that help move the mechanism forward through a number of interactions including the selection of sites for cutting, splicing, and editing. DNA base sequences play roughly the same role in producing non-coding RNA molecules as they do in polypeptide construction. See e.g., Mendes, Soares, Valcárcel [2006].

[17] CUC, AGC, GUU, and ACC, could be read as anti-codons followed by two members, AU, of an anti-codon whose third base is located to the right of our string. Alternatively, C could be read as the last base of an anti-codon whose other bases are to the right of the

alternative nucleotide sequences, it is neither plausible nor illuminating to think of it as the replication of any specific DNA codon pattern. Further failures of pattern replication result from a variety of editing, erasing and other processes. If all goes well, a pattern once filled by DNA bases will be replicated by an amino acid sequence completed in its final step. But that pattern is by no means unambiguously instantiated at every step of the process.

The leech's pressure escape reflex provides even more vivid examples of information transmission without pattern replication. It's pressure sensing neurons synapse on interneurons. The interneurons synapse on the motor neurons that drive muscle fibers. Each interneuron receives inputs from sensory neurons that originate at different locations on the leech's body. Because they are subjected to different pressure stimuli they fire at different rates or intervals. To produce information to transmit to motor neurons, interneurons must process and resolve the multiple inputs they receive from sensory neurons. (Churchland and Sejnowski [1992] p. 34) As a result temporal organizations of sensory and interneuron spike trains are too different to be usefully construed as instances of the same spatial or temporal pattern.[18]

Teleology is essential to our alternative to Crick's pattern replication story. As Ruth Millikan emphasized, in order to understand what makes biological information *information* one must consider its role in directing DNA expression toward the production of precursors of needed proteins. (Millikan [1993] p.186]. As things stand before a DNA segment is selected for transcription the mechanism can be set in motion toward the production of many different protein precursors. The selection and transcription of a specific DNA segment in response to a specific need drastically reduces the number of results that could otherwise have been produced and promotes the

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string. If so, the complete anti-codons would be UCA, GCG, UUA, CCA, followed by U. Another alternative would be CA followed by CAG, CGU, UAC, and CAU. (Alberts et al. [2002] p. 336)

[18] We ignore highly contrived, mathematical definitions of higher level variables produced just for the purpose of describing trivially similar patterns that are of no particular functional significance.

production of results that move the mechanism toward the assembly of the teleologically appropriate protein precursor. If all goes well the activities that entities engage in at subsequent steps eliminate more and more teleologically inappropriate results until the appropriate amino acid string has been assembled. Had a segment encoding a different protein precursor been selected, the mechanism would have eliminated different possibilities and promoted different results.

We will use the term 'function indicator' to refer to features like termporal organizations of leech reflex spike trains and arrangements of codon bases of entities and activities in mechanisms like DNA expression and the leech reflex. Like Crick's replicated patterns, they help direct the operation of the mechanism toward teleologically appropriate results. But they do not supply direction after the manner of a series of pattern replications, or a navigational map, an architectural plan, a diagram, a recipe, or any other sort of representation of the relevant result. Nor do they convey semantic content. Instead, they help move the mechanism toward its goal by determining or limiting the causal influences that the entities or activities they belong to can bring to bear on other components of the mechanism. For example firing rates or temporal distributions of action potentials determine what causal influence a pre-synaptic spike train can bring to bear on a post-synaptic neuron or muscle fiber to move the leech reflex toward its goal of getting the leech away from a putatively harmful environmental influence. The teleological significance of the relevant temporal features and the way in which they guide the reflex depend upon their causal history. When the reflex mechanism operates properly under conditions conducive to its serving its purpose, the temporal organization of sensory spike trains varies with the locations of pressure sensors relative to the part of the leech's body that is pressed. As a result, the function indicating temporal features of sensory spike trains vary with location and intensity of the pressure source and therefore with the direction in which the reflex must move the leech to serve its purpose. The causal influence that sensory spike trains exert on interneuron spiking depends upon their function indicators; interneurons don't respond in the same way to sensory inputs that differ with regard to their temporal organization. When all goes well

sensory neurons are thus constrained by their function indicators in such a way as to promote interneuron electrical activity that moves the mechanism closer to its goal. The same holds for function indicators on interneuron and motor neuron spike trains. Thus upstream function indicators influence the production of downstream function indicators. This, together with the constraints function indicators impose on the activities that entities engage in accounts for the goal directed reach of first step factors in the leech reflex. This is how sensory spike trains provide the organism with information about the location of the harmful stimulus that it needs in order to move away from that stimulus. In this sense it is information about what direction to move to avoid a pressure source.

In our other example DNA segments are expressed to supply proteins needed by the organism or one or more of its subsystems on a regular or temporary basis. The expression mechanism is set in motion by transcription factors and other molecules made available and set to work in response to specific needs.[19] The part they play in selecting and beginning the transcription of DNA segments that encode teleologically appropriate protein precursors is roughly analogous to the role pressure stimuli play in setting up teleologically appropriate spike trains in leech pressure sensors. Nucleotide bases and their spatial arrangements are the function indicators that belong to DNA codons. Their contribution to transcription is analogous to the contribution of teleologically significant temporal features of leech pressure sensor spike trains. We call such things function indicators because when all goes well they and the constraints they place on the operation of their bearers are indicative of the functions that entities and activities must carry out in order for the mechanism to serve its purpose.

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[19] Emi Iwatani objected in discussion that during the very earliest stages of the embryological process, it can be quite unclear which goals are served by the transcription of one specific DNA segment rather than others. For example, before the development of a distinct anterior-posterior axis, rudimentary organs, and distinct dorsal and ventral regions, it's hard to say just which goal is served by the synthesis of a protein that will eventually contribute to the establishment of a a midline, or a head. We don't at present know how to apply our account of function indicators and mechanistic information to such cases without begging teleological questions.

Mechanistic information is the causal influence that entities and activities at one step in the operation of a mechanism exert to select teleologically appropriate results for production in one or more subsequent steps. In short, mechanistic information is selective causality. The mechanistic information transmitted by a segment of DNA or RNA consists in its contribution to such processes as assembling, cutting and splicing strings of nucleotides. In this case mechanistic information is transmitted through bonding and bond breaking. The DNA and RNA segments are constrained by their function indicators to transmit information that moves the mechanism toward the production of precursors of needed proteins. It is information for protein production.[20] Function indicators constrain the influence of spike trains at every step of the leech's pressure avoidance reflex to promote the selection of results that move the mechanism

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[20] As an anonymous referee pointed out, the sketch of protein precursor construction we use to illustrate our account ignores recent investigations of complicated, widespread, and diverse contributions of small non coding RNA molecules to protein synthesis. In addition to setting the mechanism of DNA expression in motion in response to the organism's needs, non-coding RNAs and other molecules participate in promotion, inhibition, splicing, reassembling, editing, and other functions. Under their influence, the same DNA segments can be expressed to construct more than one polypeptide, and contribute to the synthesis of more than one protein.( See Mendes, Soares and Valcárcel [2006]) It is plausible, as Richard Burian suggests, that the most the genome contains is instructions about how the mechanism of protein construction is

> …to respond when the information it contains is unpacked in specific contexts and settings…[T]he contingencies that go into when and how that information is unpacked, and how it is processed before or during its use cannot be specified by DNA alone. (Burian, personal communication.)

We suppose that our simplified, text book style picture is faithful enough relative to specific settings and contexts in which DNA is typically expressed to illustrate our ideas aout mechanistic information. We lack the space to consider whether or how mechanistic information figures in the contributions of non-coding RNA and other molecules to polypeptide construction in any given context.

toward the teleologically appropriate muscular responses.[21] This is information for an avoidance response.

More generally, the mechanistic information an entity or activity transmits is the causal influence it exerts on other entities or activities to select teleologically appropriate results for production and to prevent or discourage teleologically inappropriate results at one or more subsequent steps. The mechanistic information an entity or activity receives is the teleologically significant causal influence the relevant entity or activity exerts on it. To store mechanistic information is to have the ability to exert a teleologically significant influence on the selection of downstream results.

**vi. Some differences between mechanistic, Shannon-Weaver, semantic, and teleo-semantic conceptions of information.**

Some weak points of analogy hold between the selection of results produced in mechanistic informational processes and the communication of a message by Shannon-Weaver signal transmission. Like Shannon and Weaver we think of information in connection with the reduction of uncertainty. But Shannon-Weaver information is a measure of uncertainty as to which of a number of alternative possible messages or signals has been chosen for transmission, or which message or signal is to be received. If noise interferes with the signal to increase uncertainty, Shannon-Weaver information increases in the sense that more possibilities remain open (Shannon and Weaver [1998] p.19). Thus Shannon-Weaver information *decreases* as more and more of the transmitted signal reaches the receiver intact. By contrast mechanistic information is a causal influence that decreases uncertainty with regard to which of a number of alternative results a mechanism is to produce.

An important disanalogy is that mechanistic information can and often does do its work without benefit of any biological counterpart to a Shannon-Weaver signal (e.g., a sequence of electrical pulses) that conveys a message by traveling through a channel from a

[21] The influence of sensory neuron spike trains extends throughout the operation of the reflex mechanism even though it loses some of its independence because each interneuron resolves and fires in response to inputs from more than one sensory neuron.

transmitter to a receiver. For example, we saw that no single sequence of electrical of electrical spikes moves (or is duplicated) intact from pressure sensors through interneurons and motor neurons to muscles in the leech reflex. Thus we reject Crick's characterization of a 'flow of information' specifying an amino acid as a flux analogous to a flow of energy or a flow of matter (Crick [1958] [pp.133-4). We maintain that his talk of information flow should be replaced by descriptions of causal and teleological relations between function indicators and mechanistic information.

Shannon-Weaver information has no semantic meaning.

> …[T]wo messages, one of which is heavily loaded with meaning and the other of which is pure nonsense can be exactly equivalent …as regards [Shannon-Weaver] information. (Shannon and Weaver [1998] p.8)

Mechanistic information lacks semantic content for a different reason: neither mechanistic information nor function indicators are, or function as symbols. An instance of mechanistic information is meaningful in the sense that it selects results to move a mechanism toward its goal. But in doing so it functions as the causal influence it is, not as a symbolic representation e.g., a description, recipe, plan, map, or set of instructions.[22] One can of course use semantically meaningful expressions to describe the results that information selects. However, that is no reason to think that mechanistic information is, or consists of symbols belonging to a language. Nor is it any reason to think that mechanistic information has syntax, signification, a pragmatics, or an inferential role. One can produce a semantic representation of a home run pitch and the features that explain how the batter hit it into the stands. But that is no reason to think the pitch has semantic content (e.g., that it expresses instructions) for the bat to receive and respond to. Similar considerations hold, of course, for function indicators.[23]

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[22] Pace Stegman [2005]

[23] The fact that semantic notions don't fit the processes by which mechanistic information contributes to the selection of results to be produced argues against construing biological information on the model of Millikan's inferential account of how signs represent. Ignoring details, Millikan thinks that a sign, s, carries information about

Ruth Millikan's early bio-semantic account of information proposed that informational content depends upon the evolutionary history of the mechanism in whose operation it figures (Millikan [1993] pp. 83-102). Our main objection to this is that it rules out attributing information or identifying its significance to the continuity of mechanisms whose evolutionary history is unknown or irrelevant. Moreover, biologists typically don't rest their cases for claims about the function of a mechanism or the role of information on theories about the adaptive value or evolutionary history of it or similar mechanisms. Crick knew that DNA expression and genetic coding were important to variation, adaptation and natural selection. But his account of the role of genetic information in protein synthesis neither implies nor assumes any specific account of how the mechanism of DNA expression evolved. The same holds for investigations of sensory-motor reflexes since Sherrington. Investigators typically don't need to find out how a mechanism evolved in order to develop or test accounts of its function and its use of biological information. Indeed, they sometimes rely on what they know on independent grounds about a mechanism's function and the purposes it serves to draw conclusions about its adaptive value or evolutionary history.

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something, r, only if there is a "natural connection" between s and r such that a system that is properly attuned to the connection can do something analogous to inferring r from s. For example, she thinks a mitten she found on the path outside her house carries information about her daughter's whereabouts for anyone who knows enough to infer that her daughter's having come home and dropped it on the way in is the best explanation of how the glove got there.(Millikan [2004] p. 37) Millikan characterizes the inferential process as a matter of "tracking" the connection between the glove, and the daughter or her whereabouts.*(ibid)* Although there certainly are cases in which signs are said to carry information about something by virtue of what we can infer from them, it sheds no light on biological information to think of DNA codons or leech spike trains as signs from which the relevant mechanisms draw conclusions about what results they should produce. Such inferences would be impossible unless the spike trains or codons carried information with semantic content or the expression or reflex mechanisms produced semantically meaningful descriptions of the codons or spike trains to draw conclusions from. If any tracking goes on in DNA expression or leech bending, the tracking must be understood non-inferentially in terms of function indicators and the teleologically significant influences they enable their bearers to exert.

A further difficulty for bio-semantics would come with a claim that a mechanism can use information only for purposes it was naturally selected to serve. Adapting an example of Rick Grush's, imagine two leeches with similar nervous systems and other body parts living in similar environments with similar predators, food sources, etc. and similar needs for self maintenance. Suppose their nerves and muscles behave in the same way to produce the same responses to the same pressure stimuli, according to bio-semantics, they could not transmit the same information if their neuro-muscular systems did not evolve in the same way. Suppose one of them is an artificial leech designed and assembled by engineers who gave no thought to how or whether its nerves and muscles might function to benefit it. According to bio-semantics its sensory neurons could not carry information even though they behave in exactly the same way as their counterparts in the natural leech and benefit both leeches by helping them escape environmental perils (Cf. Grush [2001] p. 166ff).

*Mechanistic information* is subject to no such difficulties. Even though it is to be understood teleologically, the goals it serves need not be fixed by any evolutionary history. Many biological mechanisms function to promote goals that are learned or acquired during the individual organism's career rather than having been evolutionarily conferred on the species it belongs to. They often serve to promote the satisfaction of temporary desires.[24] Factors whose presence is susceptible to evolutionary explanation often serve mechanisms without determining the purposes they function to serve.[25] And

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[24] A number of mechanisms belonging to Venus and Serena Williams function from time to time to promote the goal of winning a tennis tournament. Evolutionary psychology and socio-biology to the contrary, there is no good reason to think that evolutionary history accounts for their pursuit of that goal.

[25] For example, voltage gated channels which control the flow of electrical currents carried by $K^+$ ions through neuron membranes are similar enough to voltage gated $K^+$ channels in certain bacteria membranes to suggest that the former evolved from the latter. But the mechanisms these channels belong to have remarkably different functions (MacKinnon, R. [2003]).

as we said, investigators may have to learn how a biological mechanism functions and what goals it serves before they can begin to draw conclusions about its evolutionary history.[26]

**vii**. **Mechanistic information and malfunction**. We have been describing the role of information in prototypically successful operations of mechanisms like DNA expression and leech bending. But some mechanisms malfunction to produce results that make no contribution to, or run contrary to the achievement of goals they would promote if they were functioning as they should. The expression of the mutant gene responsible for cystic fibrosis is an example of the role that mechanistic information can play in the kind of malfunction we have in mind.

Cystic fibrosis is caused by a mutation in a DNA segment that encodes the precursor of a protein involved in transporting chlorine ions through cell membranes. Without that protein, chlorine ions are trapped inside lung cells where they promote an unhealthy accumulation of mucous. In sweat ducts chlorine ions are trapped outside cells. There they attract sodium ions to produce an abnormally high concentration of salt in perspiration. Both cystic fibrosis mutants and their counterparts in healthy subjects are expressed to supply a protein the organism needs. Mutant cystic fibrosis proteins could further the attainment of the organism's goals if they could get to the plasma membranes

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[26] An anonymous reviewer asks whether one can reject evolutionary accounts as we do without treating goals and proper functioning as relative to investigators interests in such a way that there is no objective fact of the matter as to which of a number of possible alternatives is the goal that a mechanism operates to promotes. Biologists often approach such questions by asking what contribution the mechanism of interest makes to functions (involved in processes as various as nutrition, respiration, hair and fingernail growth, body temperature regulation,
and disease resistance) which can be identified without appeal to evolutionary history. For example, we submit that there are facts of the matter about the proper functioning of neuronal systems such that there are objective but non-evolutionarily based answers to such questions as whether temperature regulation is the main function of the brain as Aristotle thought (Aristotle [1991] pp.1015-18), or whether the lung's main contribution to an animal's life is respiration. How such facts are established and how disputes about them are adjudicated is a topic for another paper.

of the cells that need them. But structural abnormalities in the mutant proteins trigger a quality control mechanism that discards them before they reach their destinations (Alberts et al [2002] p.631, 728). Thus the result that completes the operation of the expression mechanism in a cystic fibrosis patient prevents rather than promotes the attainment of the goal the properly functioning mechanism serves. But in many respects information plays the same role in the malfunctioning mechanism that it would play if the mechanism were functioning properly. In both cases DNA segments are selected for transcription in response to the organisms need for $Cl^-$ transport proteins. In both cases they transmit information to move the mechanism toward the satisfaction of the same need. Thus the teleological structures of the healthy and the malfunctioning mechanism are surprisingly similar. The only difference is that because the cystic fibrosis gene encodes a defective protein, the result of its expression fails to promote the goal for the sake of which the mechanism operates.

**viii**. Conclusion

We have tried to describe the ways in which and the reasons for considering some mechanisms as carrying mechanical information. Basically, the claim is that some mechanisms carry information about upstream stages that is used to produce what is needed by the organism (or system) downstream. The causal specificity of these selective influences produce what is needed to fulfill a goal or purpose. We have tried to detail these functions in terms of reach (independence and strength of influence), and most importantly the teleology of the information carrying mechanism. It is because of these features that mechanistic information supplies a unique from of continuity for the working of certain mechanisms.

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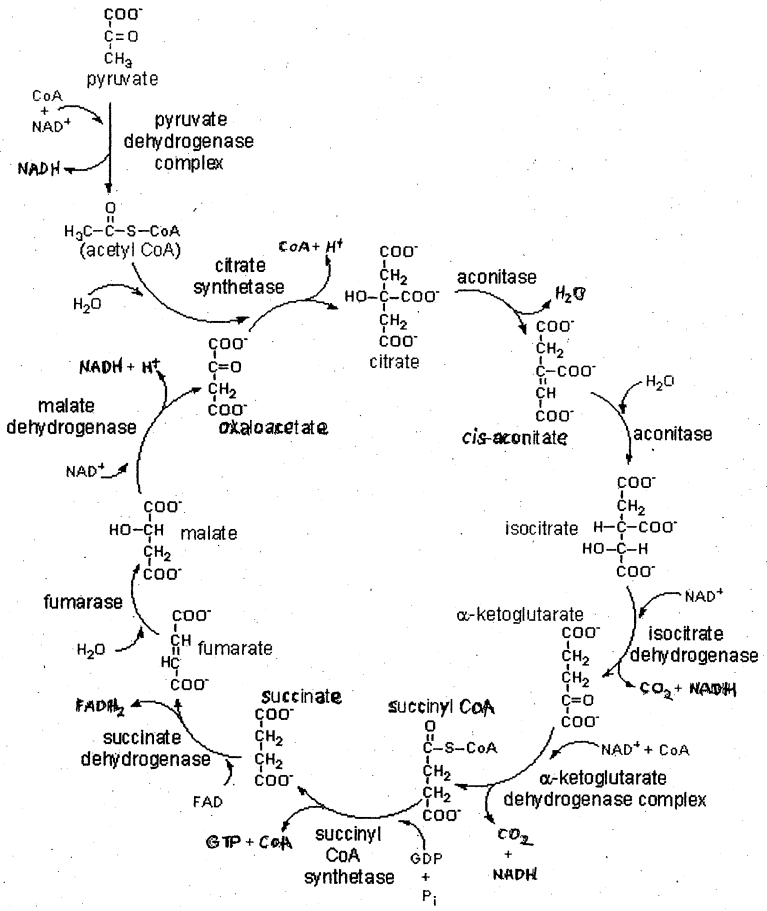
pyruvate
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NADH
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(acetyl CoA)
H2O
citrate synthetase
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citrate
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H2O
cis-aconitate
aconitase
isocitrate
NAD+
isocitrate dehydrogenase
CO2 + NADH
α-ketoglutarate
NAD+ + CoA
α-ketoglutarate dehydrogenase complex
CO2 + NADH
succinyl CoA
GDP + Pi
succinyl CoA synthetase
GTP + CoA
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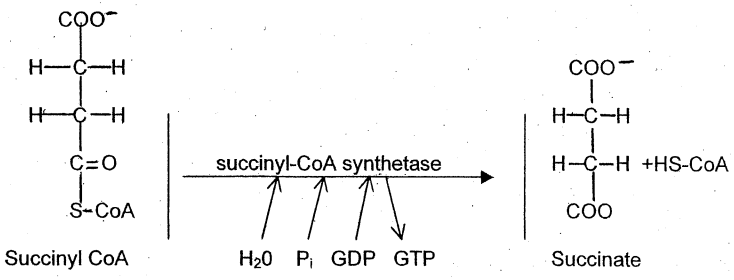
succinyl-CoA synthetase
H20 Pi GDP GTP
+HS-CoA
Succinyl CoA
Succinate

**Step 5**